Vol. 113. Pt. 10. Pp. 217–248. 32 figs. 1 Plate. 20th October, 1961

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CONTENTS

	PAGE
Badcock, Ruth M., The morphology of some parts of the head and maxillo-labium in larval Trichoptera with special reference to the Hydropsychidae	217–248, 32 figs., 1 plate

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PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7.

Price 16s. 0d.

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THE MORPHOLOGY OF SOME PARTS OF THE HEAD AND MAXILLO-LABIUM IN LARVAL TRICHOPTERA, WITH SPECIAL REFERENCE TO THE HYDROPSYCHIDAE

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Manuscript received 4th April, 1961

(Read 3rd May, 1961)

With 1 Plate and 32 Text-figures

Contents

PAGE

I. Introduction 217
II. Technique 218
III. The apotome 218
IV. The maxilla 223
V. The labium and ventral, or posterior, head sclerites . . 230
(1) Median labial sclerites and gula controversy . . 230
(*a*) Terminology in the literature 230
(*b*) The posterior tentorial pits 231
(*c*) The " protogula ", ventral margin of the occipital foramen, postgenae and phylogenetic considerations 232
(*d*) The prementum, postmentum and hypopharynx 242
(2) The labial palps 244
VI. Acknowledgments 244
VII. Summary 244
VIII. Abbreviations used in the figures 246
IX. References 246

I. Introduction

There is considerable confusion regarding the terminology of the parts of the maxillo-labium in caddis larvae, and this accounts for some of the discrepancies in published work. The interpretation of some parts of the head capsule is also controversial. It was thought desirable to study these matters before publishing descriptions of hydropsychid larvae, and the condition in these larvae has been compared with that in other larval Trichoptera and in allied orders. So it is hoped that, besides providing clarification and a justification for the terminology which it is proposed to use in describing hydropsychids, this paper may be of some general interest to students of Trichoptera.

The points discussed are :

(1) The nature of the apotome, *i.e.* the facial area carved out by the anterior branches of the ecdysial cleavage line (or frontal sulci), and the form of the tentorium.

(2) The subdivision of the maxillary stipes and the presence or absence of a palpifer, matters affecting the view taken concerning the number of segments which comprise the palp.

(3) The nature of the maxillary lobe.

(4) The interpretation of the median labial and ventral (or posterior) head sclerites, especially whether or not a gula is to be regarded as present.

(5) The number of parts in the labial palp.

II. Technique

Details of the attachment of muscles are of importance in identifying parts; microdissection of the larval head and mouthparts with micromanipulators, under a binocular microscope, elucidated points concerning the origin and insertion of particular muscles. When examining the musculature in microscopic preparations, it was often found beneficial to use polarised light, which rendered many muscles clearly discernible even in unstained preparations. Alternatively, the material was stained with borax carmine, then cleared and mounted in polyvinyl lactophenol. In order to display the tentorium *in situ* in the head capsule, the larval head was incubated in papain solution for two days or longer, after which the muscles were partially digested and came away when the head was boiled in 5 per cent. caustic potash solution. Then, after washing, dehydrating and final clearing of the head in polyvinyl lactophenol, the tentorium showed through distinctly.

For section cutting, needed to reveal tentorial pits, the larval head was first fixed in Carnoy-Lebrun, washed in alcohol, then cleared in cellosolve prior to infiltration with ester-wax. Early efforts, in which the material was only infiltrated for 24 hours before embedding, did not give satisfactory sections, but good results were obtained after infiltration for 42 hours. Meyer's albumen was found to be an inadequate adhesive for isolated strips of chitin, and at times sections of only the apotome were attempted, but Haupt's adhesive, rendered insoluble and hardened by flooding with 4 per cent. formalin (which also served for flattening the sections), was most efficient. The sections were successfully stained with Mallory's triple stain after flattening, drying and removal of the wax.

III. The Apotome

The apotome of caddis larvae has been variously called the clypeus (Ulmer, in all his larval descriptions; Lestage, 1921; Cook, 1944; Hickin, 1946 and throughout his subsequent larval descriptions; Macdonald, 1950; Philipson, 1953), the frons (Lloyd, 1921; Orcutt, *in* Betten 1934), and the frontoclypeus (Krafka, 1923; Nielsen, 1942, 1948; Mackereth, 1954, 1956; Hanna, 1956). Snodgrass (1947) regards it as frontoclypeal but points out that in trichopterous larvae the ecdysial cleavage line passes median to the antennae, so that some of the clypeal and frontal regions may lie outside the apotome.

According to Snodgrass (1947), in general, when an epistomal sulcus is present, it separates the frontal and clypeal areas from each other, but in its absence the two areas are to be identified by the muscles arising on them. These muscles are said to fall into two main groups relative to the position of the frontal ganglion. Below or anterior to the frontal ganglion there are the cibarial muscles, and the part of the cranium on which they originate is the clypeus. The group of muscles above or posterior to the frontal ganglion comprises the labral muscles, frontal muscles of the hypopharynx (derived from mouth angle retractors) and precerebral dilators of the pharynx. This group originates on the frons.

Although Snodgrass' criteria may not be infallible, it was considered desirable to investigate them further with particular reference to the Hydropsychidae. It seemed that there were two lines of evidence to be pursued, firstly to see if there was any trace of an epistomal sulcus, and secondly to find the position of the frontal ganglion and the attachment of muscles relative to this ganglion. The anterior tentorial pits always lie in the subgenal or the epistomal sulcus, more usually in the latter (Snodgrass, 1935) and so the position of these pits is relevant in determining the location of an epistomal sulcus. This led me to a study of the tentorium in caddis larvae. Krafka (1923) states that it is reduced, consisting of a pair of fibre-like arms extending through the head from the dorsal to the ventral wall, a tentorial body being absent in the later larval stages, although he found one in an early instar of *Mystro-*

phora americanum Banks. However, Hinton (1958) maintains that a very slender tentorial bridge is present in larval Trichoptera and has previously been overlooked. Apart from Krafka's reference to *Mystrophora*, neither writer supports his general statement with instances of the specific material on which it is based. My own results reconcile the two statements by showing a differential condition in larval Trichoptera, a tentorial bridge being present in some forms and absent in others. A relatively strong bridge was present in well-grown larvae of *Agapetus comatus* (Pict.) (fig. 1). A slender tentorial bridge was found in well grown larvae of: *Chimarrha marginata* (L.), *Polycentropus* sp., *Rhyacophila dorsalis* (Curt.) (fig. 2), *Phryganea varia* Fab. (bridge relatively well developed and conspicuous), *Limnophilus* sp., *Halesus* sp., *Anabolia nervosa* (Curt.), *Odontocerum albicorne* (Scop.) and *Molanna angustata* Curt. No tentorial bridge was present in well-grown larvae of *Notidobia ciliaris* (L.) (young instars were not examined), or in either early or later instars of British hydropsychid larvae; species examined were: *Hydropsyche angustipennis* (Curt.), *H. pellucidula* (Curt.), *H. contubernalis* McLach.,[1] *H. fulvipes* (Curt.), *H. instabilis* (Curt.) and *Diplectrona felix* McLach. In view of Hinton's statement, particular care was taken with the hydropsychids to ensure that the bridge had not been overlooked. Many heads were prepared and examined, and sections were also studied, but I am satisfied that a tentorial bridge is absent in these hydropsychid larvae.

Preparations of heads displaying the larval hydropsychid tentorium *in situ* showed that it consists only of fibre-like right and left tentorial arms which remain quite separate from one another. As shown in figures 3, 4 and 5, each posterior arm arises posteriorly on the ventral surface of the head and extends anterodorsally within the head to unite with the anterior arm of that side, an arm extending from a point on the apotome somewhat median to the ecdysial cleavage line; this point of origin in hydropsychids is in marked contrast to that of most other caddis larvae, in which the anterior arms extend from a point actually in the cleavage line, often at its inflection, as in *Rhyacophila dorsalis* Curt. (fig. 6, *a.t.p.*).

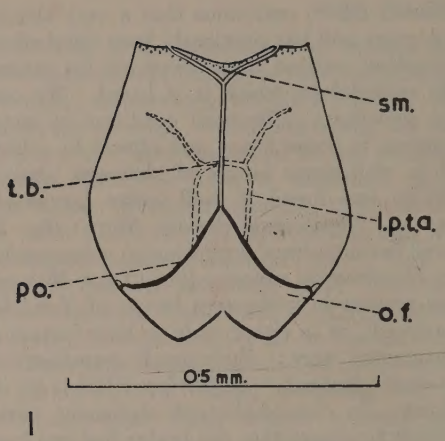
Krafka (1923) refers to the junctions of the antero-dorsal tentorial arms with the cranium as the pretentorinae, *i.e.* the anterior tentorial pits. From their position, I wondered whether these arms might in fact be the dorsal arms, reaching the cranium at dorsal maculae, the true anterior arms being absent. However, detailed examination of larval heads and sections failed to reveal any other structures which could be anterior tentorial pits elsewhere on the head and, furthermore, sections passing through the tentorial arms at their junction with the cranium showed that these arms were in fact arising from definite pits, not maculae, so that these points are correctly regarded as the anterior tentorial pits and the arms as anterior arms, not dorsal ones.

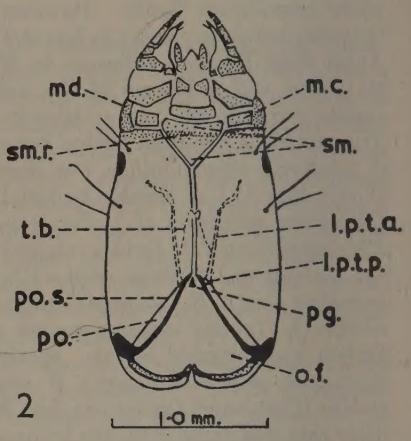
In the British hydropsychid larvae a line (figs. 5 and 7, *e.s.*; Plate I), connecting each anterior tentorial pit with the ecdysial cleavage line is always present, although its degree of distinctness varies and it may be overlooked. It is much more readily recognisable as a sulcus in the known British larval species of *Hydropsyche*[2] than in larvae of *Diplectrona felix* and *Cheumatopsyche lepida* (Pict.), but even in these forms careful search revealed a line which could justifiably be interpreted as a sulcus, while in larvae of the Japanese hydropsychid *Macronema radiatum* McLach.[3] a very distinct sulcal ridge is present in this position between the cleavage line and the pits. In some individuals of larval *Hydropsyche* there appeared to be a slight line passing from one anterior tentorial pit to the other in a gentle, posteriorly arched curve

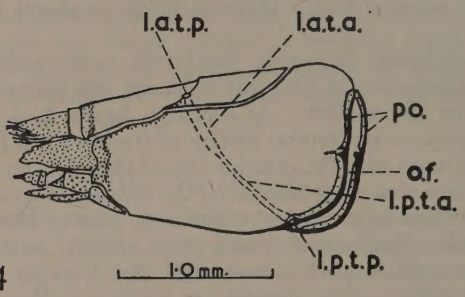
[1] I recognise Kimmins' (1957) splitting of *H. ornatula* McLach., whereby the British form becomes *contubernalis*.

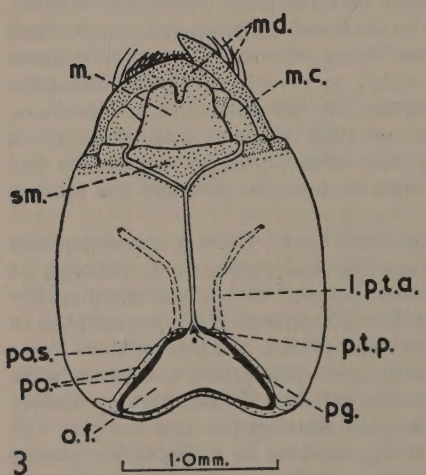
[2] *Hydropsyche pellucidula* (Curtis), *H. saxonica* McLach., *H. angustipennis* (Curtis), *H. contubernalis* McLach., *H. instabilis* (Curtis), *H. fulvipes* (Curtis).

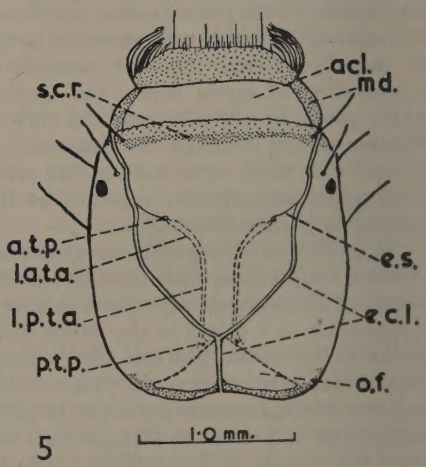
[3] I am indebted to Dr. M. Tsuda for larvae of *Macronema*.











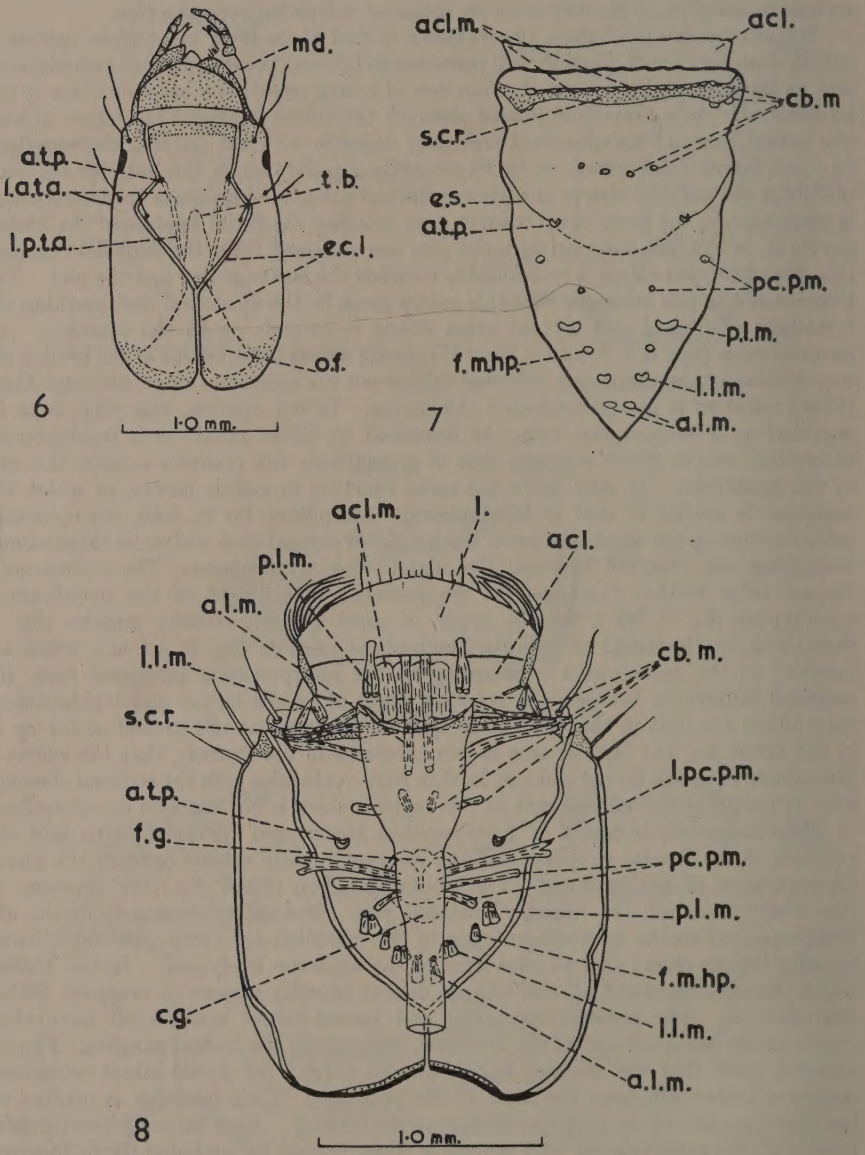
FIGS. 1–5.—Heads of last larval instar treated to show tentorium and viewed with transmitted light: (1–3) Ventral views of: (1) *Agapetus comatus* (Pict.); (2) *Rhyacophila dorsalis* (Curt.); (3) *Hydropsyche instabilis* (Curt.). (4–5) *H. instabilis*: (4) lateral and (5) dorsal views.

(Plate I), but often it consisted of hardly more than wrinkles and frequently it was absent, as is the case in *Diplectrona felix* and *Cheumatopsyche lepida*, so it seems unwise to attempt to identify even an incipient sulcus between the pits.

My interpretation of these observations is that there is an incomplete epistomal sulcus which is arched, passing well posterior to (above) the mandibular articulations, and as its ridge no longer has the function of acting as a brace between these it can be reduced. As a functional line of strength the sulcus is absent laterally—indeed, the lateral part of this epistomal arch may coincide with the ecdysial cleavage line. In most larval Trichoptera, as in *Rhyacophila dorsalis*, where the anterior tentorial pits lie in the ecdysial cleave line (*cum* epistomal sulcus), no separate epistomal sulcus is recognisable, for there is no median part crossing the facial apotome. In hydropsychids, where the anterior tentorial pits are removed from the ecdysial cleavage line, the epistomal sulcus is recognisable between the cleavage line and the pits. The location of the pits indicates that this sulcus must be the epistomal one, marking the boundary of frontal and clypeal areas where it extends on to the apotome. An anterior ridge (figs. 5, 7, 8, *s.c.r.* ; Plate I) running across the apotome at the level of the mandibular articulations and subgenal sulci is not the epistomal ridge, although Cook (1944) refers to it as the epistomal thickening. In my opinion, this ridge is to be regarded as a submarginal ridge, as described by Short (1951) in a lepidopterous caterpillar, where Short suggests that it strengthens the cranium against the pull of the mandibles. It may serve the same function in caddis larvae, in which the situation is similar to that in lepidopterous caterpillars, for in both the epistomal sulcus arches up the head because of the increased clypeal area and so its ridge cannot strengthen the cranium between the mandibular articulations. The submarginal clypeal ridge further functions for the posterior attachment of the membranous anteclypeus (fig. 8, *acl.*), for the origin of some anterior cibarial muscles (fig. 8, *cb.m.*) and for the origin of delicate longitudinal muscles (fig. 8, *acl. m.*), which are inserted on the anteclypeus. According to the interpretation presented here, the essential differences between the relevant parts of caddis larvae and lepidopterous caterpillars are that in the former the epistomal sulcus has not arched as far up as in the latter (*i.e.* the clypeal area is less extensive in the former), that the sulcus is incomplete in caddis larvae and—at least in part—coincides with the ecdysial cleavage line, so that it is virtually absent in this region, which is not the case in caterpillars.

Microdissection of heads of hydropsychid larvae and *Rhyacophila* to find the position of the frontal ganglion and the relevant muscle origins confirm the above interpretation of the apotome. The frontal ganglion (fig. 8, *f.g.*) lies between, or just slightly behind, the anterior tentorial pits. Muscles stretching from the alimentary canal to the apotome anterior to this ganglion are apparently the cibarial muscles (fig. 8, *cb.m.*) and all that area of the apotome is clypeal. In the *Hydropsyche* larvae dissected,[4] all the cibarial dilator muscles appear to originate within the apotome. The anterior, posterior and lateral labral muscles all have their origin on the posterior part of the apotome, well behind the frontal ganglion. Figures 7 and 8 show that the anterior labral muscles (*a.l.m.*) (or dorsal labral retractors) originate posteriorly, near the apex of the apotome. Their insertion is median on the dorsal surface of the posterior margin of the labrum. Each lateral labral (tormal) muscle (*l.l.m.*) originates as two groups of fibres lateral to, and slightly in front of, the origin of the anterior labral muscles and passes dorsal to both the anterior and posterior labral muscles, but ventral to the anterior cibarial muscles (hence much of it was removed for figure 8 in order to display the cibarials), before its insertion on a torma. The posterior labral muscles (fig. 8, *p.l.m.*), each consisting throughout of two large, distinct groups of fibres, arise anteriorly to the origin of the lateral labral muscles and are inserted on the epipharyngeal surface of the labrum. The frontal muscles of the hypopharynx (*f.m.hp.*) (or mouth angle retractors) arise

[4] *H. pellucidula, H. angustipennis, H. instabilis* and *H. contubernalis.*



FIGS. 6–8.—(6) *Rhyacophila dorsalis* (Curt.), dorsal view of head of last larval instar treated to show tentorium. (7) Interpretation of Plate I, apotome of *Hydropsyche pellucidula* (Curt.), last (fifth) larval instar, showing muscle impressions. (8) Internal view of dorsal surface of larval *Hydropsyche* head, dissected to show muscle attachments, based on fifth instar larvae of *H. pellucidula*, *H. angustipennis* (Curt.) and *H. instabilis* (Curt.).

between the origins of lateral and posterior labral muscles. The slender muscle which Hinton (1958) mentions as arising on the clypeus and being inserted on the apex of the torma in a hydropsychid larva may, as he suggests, be a cibarial muscle which has shifted its insertion.

Precerebral pharyngeal muscles (fig. 8, *pc.p.m.*, *l.pc.p.m.*) which are inserted dorsally on the pharynx and pass within the loop formed by the cerebral connectives of the frontal ganglion, all have their origin on a part of the cranium behind the frontal ganglion and anterior tentorial pits in these larvae. This area of the apotome behind the anterior tentorial pits is to be regarded as frontal. It is, however, to be noted that, as found by Hinton (1947) in lepidopterous caterpillars and trichopterous larvae, and confirmed by Short (1951) in caterpillars, not all the precerebral pharyngeal dilators originate within the apotome ; a pair have their origin just lateral to it (fig. 8, *l.pc.p.m.*), and in the *Hydropsyche* larvae examined the fibres of these muscles were divided into two distinct groups near their origin. In my opinion this does not invalidate Snodgrass' criteria for recognition of frontal and clypeal areas, it merely demonstrates his point that some of these areas may lie outside the apotome. It does, however, seem that, contrary to Snodgrass' statement, the arms of the cleavage line do not invariably separate the attachment of facial and mandibular muscles. Hinton and Short have both shown a further discrepancy in the lepidopterous caterpillar, namely that a pair of precerebral pharyngeal muscles originate in the area which Snodgrass designates as clypeal, but this has not been found in *Hydropsyche* larvae. While it is fully realised that Snodgrass' criteria are not to be regarded as infallible, it is nevertheless considered that, by and large, they still stand as useful morphological guides towards the identification of frontal and clypeal areas.

As all types of evidence are in accordance with the interpretation presented above, I have no hesitation in regarding the trichopterous apotome as fronto-clypeal in these larvae.

IV. The Maxilla

In the maxilla the chief points of controversy are :

(1) The interpretation of the parts of the maxillary palp and stipes, *i.e.* whether :

(*a*) a palpifer exists ; or

(*b*) the stipes is transversely divided into basistipes and dististipes, as maintained by Hinton (1958) for all the panorpoid orders ; or

(*c*) the stipes is undivided—comprising solely the sclerite designated by Hinton as basistipes—and all the sclerites distal to it which relate to the palp should be described as palpal segments.

(2) Whether the lobe of the maxilla represents the galea or the lacinia of other insects, or a fusion of the two.

Crampton (1921 : 84–85 ; 1928 : 1) followed Hansen (1893) in considering that insects evolved from Crustacea and that a palpifer represented a segment in the insect mouthpart limb with the galea as its endite. According to Crampton (1921 : 86) a palpifer occurs in the maxilla of larval Trichoptera and the endite present represents the galea.

However, Snodgrass (1928) regards a palpifer as a secondarily differentiated region of the stipes, supporting the palp ; he states " that the palpifer is not a segment of the appendage is shown by the fact that muscles neither arise within it nor are inserted upon it " ; and also (Snodgrass, 1932 : 481) " The origin of the palpus muscles in the mesal part of the stipes and the origin of the galea muscle in the base of the stipes also leave no support for the idea, held by some writers, that the palpifer is a segment of the appendage bearing the palpus and the galea ".

Nielson (1942 and 1948) follows Crampton's terminology, recognising a palpifer in larval Trichoptera and calling the lobe the galea. He finds in addition (1942)

a rudimentary lacinia in certain caddis larvae such as *Wormaldia* and *Plectrocnemia* and also maintains that " Bei *Ecclisopteryx*, *Apatania* und *Silo* is die Lacinia ebenfalls wohl entwickelt, vom Stipes aber weniger deutlich abgesetzt und hat kein Sklerit." I do not find Nielsen's " lacinia " very convincing as such and would prefer to regard this minute unsclerotised projection—which even in *Plectrocnemia* has no clear demarcation from the stipes—as a part of the stipes and not a lacinia. Nor would I regard the structure which Nielsen (1942 : 285) describes in larvae of *Odontocerum* and the Limnophilinae as a stipital appendage comparable to a lacinia, which is his interpretation. In larvae of *Halesus* sp., it would seem rather to be a median stipital

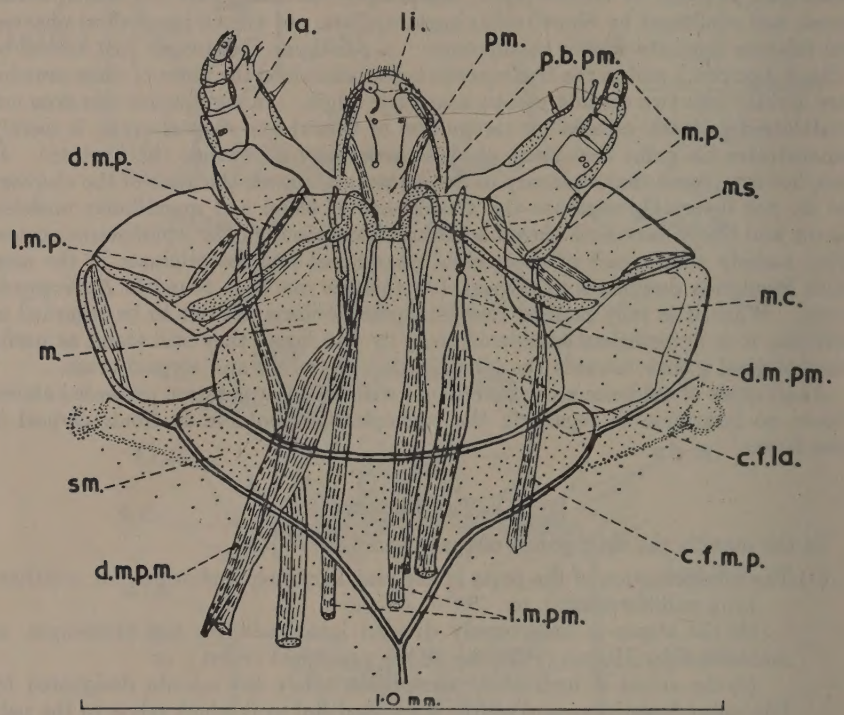


FIG. 9.—Maxillo-labium of *Hydropsyche pellucidula* (Curt.), fifth instar larva, ventral view of preparation seen with transmitted light and showing some of the muscles and their attachments.

dilation, and indeed the same sort of dilation also occurs on the outer, posterior surface of the stipes, although to a lesser extent. Nielsen does not support his terminology by any consideration of musculature and is evidently unaware of the work of Das (1937).

Das, from his investigations of the musculature of the mouthparts of insect larvae, concludes that " in larval Trichoptera the lobe is the lacinia ". He dismisses the suggestion of Orcutt (in Betten, 1934) that it is the fused lacinia and galea, since it does not show any sign of external demarcation such as is found in the fused lacinia and galea of *Thanatophilus*, *Panorpa* and *Rhaphidia*. Further, Das maintains that there is no palpifer in larval Trichoptera, interpreting the palpifer of other writers as the basal part of the palp.

Hinton (1958) refers to the " maxillary lobe " of the Trichoptera, saying that it is undivided. He maintains that in the Panorpoidea the transverse division of the

stipes into basistipes and dististipes is a primitive feature. His " dististipes " corresponds to the sclerite hitherto regarded either as a palpifer or as the basal segment of the palp. He states that " In many Trichoptera the dististipes is particularly large and sharply delimited ; it is in no sense a basal segment of the palp but is often as long and nearly as broad as the basistipes ". The muscles which are usually regarded as associated with the palp are interpreted by him as muscles of the dististipes and he maintains that " muscles are never inserted in either the maxillary or labial palpi of any larvae of the Panorpoidea ". Similarly he regards the cranial flexor of the maxillary lobe as the cranial flexor of the dististipes in the Boreidae, Trichoptera and

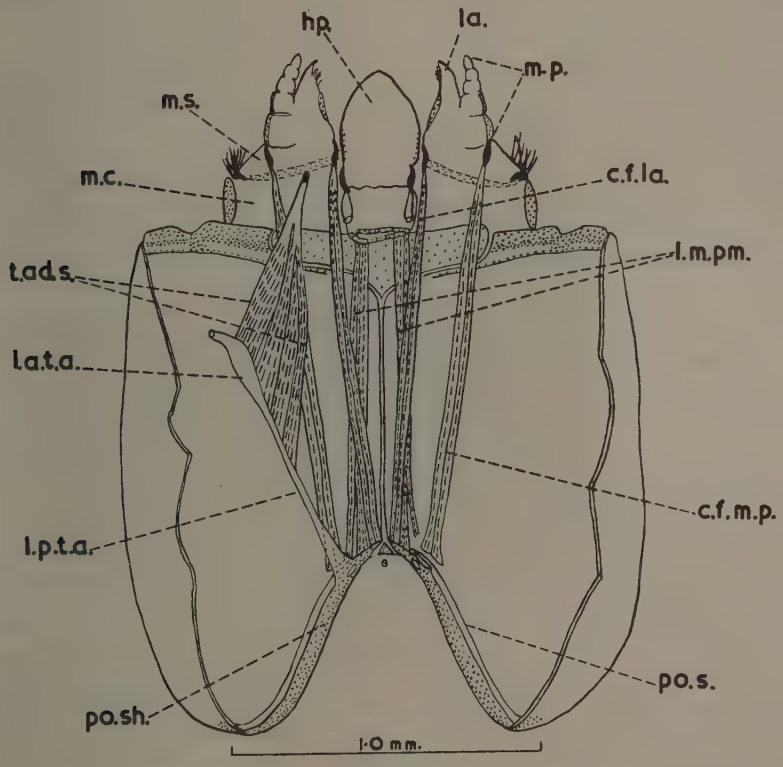


FIG. 10.—Internal view of ventral part of *Hydropsyche* sp. fifth instar larval head, dissected to display some of the muscles of the maxillo-labium. Right tentorial arms and attached muscles removed.

primitive Diptera and as the cranial flexor of the cardostipes in the Panorpidae, Choristidae, Bittacidae and Siphonaptera, although agreeing that it is homologous with the cranial flexor of the lacinia in less specialised insects. Although, as Hinton rightly says, " Muscle origins and insertions are guides to homology, they are not unquestionable proofs ", they are surely not to be dismissed summarily without strong supporting evidence. In my opinion Hinton does not provide this ; his interpretation might be a possible one but it would require further substantiation before general acceptance. Some features operating against it are discussed below, but *a priori* it seems functionally unreasonable to deprive a well-developed palp of

any muscle supply, so that its movements must be regarded as entirely dependent on those of a dististipes, and virtually to create intrinsic stipital muscles, unless the case for so doing is overwhelmingly strong.

For the present work, the morphology of the maxilla was studied particularly in the last larval instars of British species of *Hydropsyche* and in *Diplectrona felix*. Larvae, pupae or imagines of other Trichoptera were also examined for certain points (especially *Rhyacophila dorsalis*, *Plectrocnemia* and *Polycentropus*, in which the maxillary palps are large, well-developed structures), as were larvae and imagines of the neuropteran *Sialis* and the lepidopterous caterpillar *Pieris brassicae* (L.), the conditions in which were compared with descriptions in the literature and with descriptions and figures of larval Mecoptera given by Das (1937), Applegarth (1939), Bierbrodt (1942) and Imms (1944).

In hydropsychid larvae—as in the other trichopterous larvae examined—the muscles which are generally regarded as the levator and depressor (fig. 9, *l.m.p.*, *d.m.p.*) of the maxillary palp have their origins on the base of the stipes and their insertions on the base of the palp, *i.e.* on that sclerite which would be designated as " palpifer " by Crampton and by Nielsen or as " dististipes " by Hinton. The cranial flexor of the maxillary palp (figs. 9 and 10, *c.f.m.p.*) which originates on the ventral, posterior part of the cranium also has its insertion on the same sclerite at the base of the palp. The insertion of these palpal muscles is similar in lepidopterous caterpillars, as has been shown by Das (1937) and verified by myself in larvae of *Pieris brassicae*.

In larvae of *Sialis* (Megaloptera, fig. 11) I agree with the interpretation of Das that the fifth (basal) segment of the palp has become fused with the base of the galea, although the musculature remains distinct. The levator and depressor muscles of the palp are inserted at the base of this fused basal section, through which the stipital flexor of the galea passes near the median border to its insertion on the free part of the galea. Also traversing this fused basal section of galea and palp, but near its outer border, is a small muscle, which is inserted on the base of the fourth (or next proximal) palpal segment and which I regard as an intrinsic muscle of the palp.

It has not been possible for me to examine larvae of either *Rhaphidia* (Neuroptera) or *Panorpa* (Mecoptera) but in both these genera Das (1937) depicts a four-segmented palp with levator and depressor muscles inserted at its base. Bierbrodt (1942) and Imms (1944) also consider the maxillary palp of larval *Panorpa* to be four-segmented and without a palpifer, but Ferris and Rees (1939) recognise a palpifer. In addition to the muscles which Das describes as inserted on the palp, Imms shows a cranial flexor of the palp inserted at its base. This is presumably the muscle which Das calls the cranial flexor of the stipes in both larval *Panorpa* and *Bibio* (Diptera), although in his drawing of the maxilla in larval *Panorpa* it appears to be inserted on the palp rather than on the stipes.

Hinton criticises the interpretations of Das and Snodgrass regarding all larvae of the panorpoid complex and especially Lepidoptera, saying " The assumptions explicit in the interpretations of Snodgrass and Das is that a palp must have muscles inserted at least in its basal segment. Both writers are unaware of the fact that muscles are never inserted in either the maxillary or the labial palpi of any larvae of the Panorpoidea ". This criticism would apply equally to Imms' (1944) interpretation of the maxillae of Mecoptera and Diptera. Hinton's interpretation might be a possible one, but I do not consider it to be adequately justified. In any case the term " Panorpoid Complex " as envisaged by Tillyard (1918–20), who originated it, includes the Neuroptera (not considered by Hinton). Now in *Sialis* larvae, even if one applies Hinton's terminology and regards the fifth segment of the palp as a dististipes to which the insertions of the palpal muscles have shifted, there is still the small muscle inserted on the fourth palpal segment. So even if one allowed Hinton's interpretation of basi- and dististipes, his statement that " muscles are

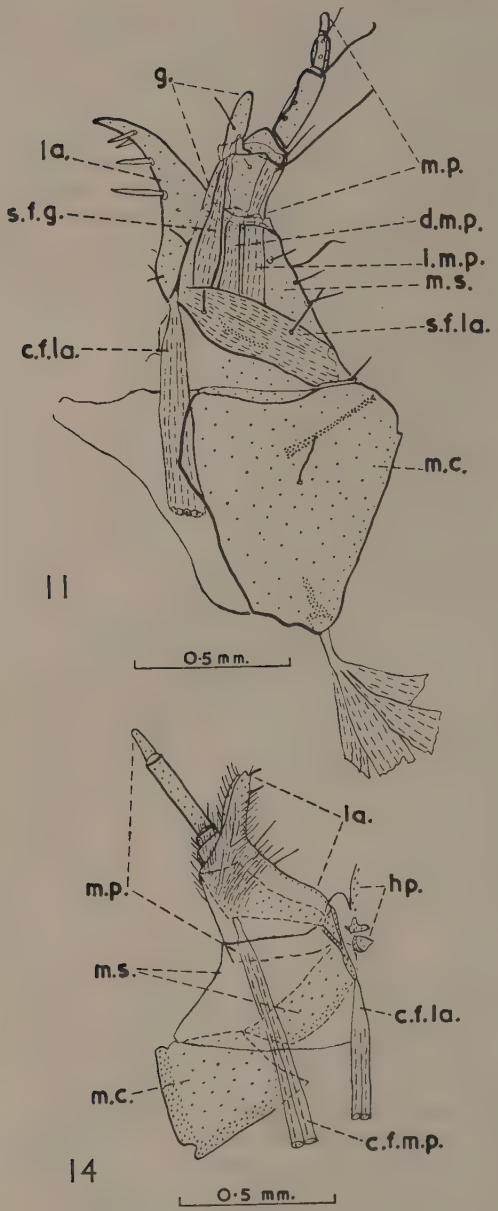
never inserted in either the maxillary or labial palpi of any larvae of the Panorpoidea " is untenable if one interprets Panorpoidea in its original and generally accepted sense. I would, however, agree with Hinton to the extent that I have not found intrinsic palpal muscles in the maxillary palps of larval Trichoptera and Lepidoptera, merely extrinsic muscles inserted on the base of the palps. Neither preparations nor serial sections revealed any intrinsic muscles, the palps appearing to be moved from the base and to be sensory structures, full of nerve fibres from the numerous sensilla. In contrast to the absence of intrinsic palpal muscles in larval Trichoptera, the pupal maxillary palp is well supplied with them. In *Rhyacophila dorsalis* the pupal palp clearly comprises five segments and both intrinsic and extrinsic muscles, the extrinsic muscles being inserted at the base of the proximal segment and both palp and lobe being subtended by the stipes. This is also true of the imago. Thus the recognition of a five-segmented palp (and no dististipes or palpifer) in the larva of *Rhyacophila* and of hydropsychids would be consistent with conditions in both the pupa and the imago.

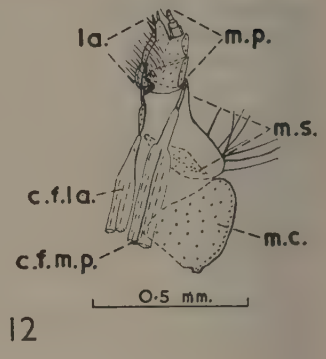
Having discussed palpal musculature, it is now appropriate to say that I propose to adhere to Snodgrass' criterion that a palpifer has no muscles arising within it or inserted upon it, and consequently prefer not to call the sclerite in question a palpifer in *Sialis* or in the trichopterous and lepidopterous larvae which I have examined.

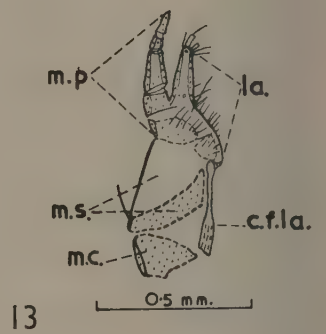
Irrespective of musculature, the size and disposition of the sclerite do not necessarily lead one to suppose that it is a part of the stipes rather than of the palp, as is stated by Hinton. Indeed in the larval hydropsychids (fig. 12), in my opinion, it looks more like a part of the palp. It is true that there is fusion between the base of the palp and the lobe, and on the outer (ventral) surface the controversial sclerite embraces the maxillary lobe to some extent, but the coverage is not complete and it does not occur on the inner surface where a fringe of fine hairs, characteristic of maxillary lobe rather than palp or stipes, is clearly visible extending across the lobe and as far proximally as the stipes (basistipes of Hinton). It would appear that although the base of the lobe may be embraced by, and to some extent fused laterally with, the sclerite in question, it is not subtended by the distal part of this sclerite as Hinton would lead one to expect but, despite fusion, retains its identity throughout the length of the two, both of which are subtended by the stipes (basistipes of Hinton).

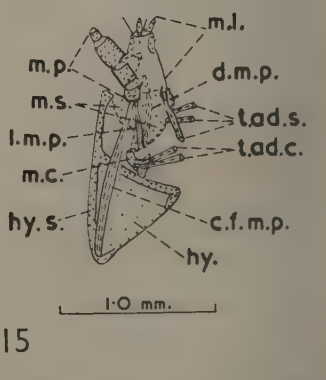
The concept of fusion between basal segment of palp and maxillary lobe, in preference to interpreting this part as dististipes, receives further support from the fact that, at least in larvae of *Rhyacophila dorsalis* (fig. 13), *Hydropsyche* spp. and *Plectrocnemia* (fig. 14), there is fusion between the fourth (or next distal) palpal segment and the maxillary lobe. Only the distal parts of palp and lobe are completely free from each other. Theories of stipital division would break down at the level of the next basal palpal segment, especially when palpal sclerite and lobe are clearly demarcated : if one has to admit fusion at the level of the fourth segment of the palp, then it is logical also to allow it in the basal segment when other facts are in accordance with this interpretation.

Despite fusion of the basal parts of palp and lobe, extrinsic muscles of the two components have retained their identity. Palpal muscles have been described above, but there is an extrinsic muscle of the maxilla, which originates on the postocciput and has its insertion on the inner edge of the base of the lobe (+ fused palpal base). This muscle has all the characteristics of a cranial flexor of the lacinia (figs. 9 and 10, *c.f.la.*) and is the only muscle of the maxillary lobe in the larval Trichoptera examined during this investigation. Now the lacinia is the only endite of the generalised maxilla that has a muscle extrinsic to the maxilla (Snodgrass, 1932, 1935 ; Das, 1937). The flexor of the galea originates on the stipes ; the lacinia may also have a muscle originating on the stipes but, as Das says, the stipital flexor of the lacinia is absent in trichopterous larvae. I suggest that this absence is correlated with fusion of lobe with base of palp ; the stipital muscles of the palp will also move the lobe.









Figs. 11–15.—Dorsal views of larval maxilla: (11) *Sialis lutaria* L. (right). (12) *Hydropsyche angustipennis* (Curt.) (right). (13) *Rhyacophila dorsalis* (Curt.) (left). (14) *Plectrocnemia* sp. (left). (15) *Pieris brassicae* (L.) (left).

Hinton has, of course, to regard the cranial flexor of the lacinia as the cranial flexor of the dististipes, thereby implying a—to me—unwarranted shift in position. The nature of the insertion of this muscle on the fused lobe + palp is worth noting. The sclerotisation of the basal part of the lacinia, as I interpret the lobe, is weak. There may, however, be a strengthening at the median rim and between the base of the tendon and the base of the palp. In larvae of *Plectrocnemia* (fig. 14) and *Polycentropus*, the latter thickening is seen as one of the prongs of the tendon, which appears to have a two-pronged insertion, the other prong being directed towards the median rim. In *Hydropsyche* spp. (fig. 12) there is a band of weak sclerotisation between the basal part of the tendon and the median extension of the sclerite encircling the base of the palp. This sclerotisation might be regarded as a part of the tendon (which also makes contact with the median border of the lacinia) or as a separate feature, the pull of the tendon having induced some slight sclerotisation in the membrane of the lobe, or possibly as an extension of the palpal sclerite. In larvae of *Rhyacophila dorsalis* there is a very distinct separate sclerite between the main sclerite of the basal segment of the palp and the main part of the tendon (fig. 13). This might be regarded as a further development of the weak sclerotisation seen in *Hydropsyche* spp. or as a separated median extension of the palpal sclerite. Further comparative investigation might throw light on this point but it is not significant for the present argument. Although the tendon attaching the extrinsic muscle of the lobe may acquire additional strengthening at its insertion by virtue of a secondary sclerotised connection with the palpal sclerite (a condition which is probably correlated with the weak sclerotisation of the base of the lobe and made possible by its fusion with the base of the palp), the salient feature is that the muscle is still clearly the cranial flexor of the lacinia with at least part of its insertion on that lobe.

Thus, on the basis of its musculature, and as there is nothing which would lead one to suppose that it represents either a galea or fused galea and lacinia, I regard the maxillary lobe of the hydropsychid and other caddis larvae which I have examined as the lacinia. This agrees with the general conclusion of Das regarding larval Trichoptera and with Crichton's (1957) view that in the imagines the maxillary lobe is the lacinia.

In larval *Sialis* both galea and lacinia are clearly represented and in larval *Panorpa* Das (1937), Bierbrodt (1942), and Imms (1944) agree in depicting both lobes with some basal fusion. Ferris and Rees (1939) also assume that galea and lacinia are both present in larval *Panorpa*—or if not, then at least there is a divided lacinia rather than a divided galea. In *Apterobittacus apterus* McLach., Applegarth (1939) concludes that the single maxillary lobe of the larva represents the lacinia, showing that this becomes the lacinia of the imago, in which both lacinia and galea are present, the galea developing in the pupa between the lacinia of the larva and the palp.

In lepidopterous caterpillars the matter is less clear. However, Tillyard (1922) showed that in the micropterygid *Sabatinca*, maxillary palp and a distinct lacinia and galea were present. In less primitive forms, Snodgrass (1935) regards all the maxilla distal to the stipes as lobe but says that its homology is difficult to determine in the ordinary caterpillar structure, although earlier (1928), he interpreted it as the lacinia. In contrast, Das (1937) says " The insertion of the palpal muscles at the base of the structure shows that it is the maxillary palpus and the lobe borne by the second segment of the palpus cannot be the galea as it was supposed to be by Crampton (1921). For the galea could not be borne by a distal segment of the palpus, unless it is proximally fused with the two basal segments of the palpus, which is improbable. It also lacks muscles and most probably is an outgrowth of the second segment of the palpus ". I agree with Das about the insertion of palpal muscles on the sclerite next distal to the stipes (fig. 15) and the presence of a palp, but do not agree that the entire structure must necessarily be palp or that fusion of the base of the lobe with the two basal segments of the palp is improbable. As shown above, it is here

maintained that this has occurred between palp and lacinia in at least some larval Trichoptera and that fusion of the base of the galea with one segment of the palp exists in larval *Sialis*. In lepidopterous caterpillars the condition has merely progressed a little further, with loss of the muscles of the lobe—and incidentally of an aid to the elucidation of its homology; the whole structure of palp + lobe is purely sensory, full of nerves from sensilla, and moved only from its base by the extrinsic palpal muscles. Although the homology of the lobe is difficult to determine in lepidopterous caterpillars, in typical imagines it is generally agreed that the lobe (forming the proboscis) is the galea, a contrast to the condition in Trichoptera.

Hinton's theory subdivides the stipes yet again in larval Lepidoptera, for he considers the dististipes to be divided into two distinct sclerites in many forms. In my opinion this interpretation is improbable and unnecessary. Thus it is considered that Hinton's interpretation of the parts of the maxilla in larvae of the panorpoid complex is not the only possibility but that the one suggested in this paper can be maintained logically in Trichoptera and other panorpoid orders, and fits the facts better.

V. The Labium and Ventral, or Posterior, Head Sclerites

(1) *Median Labial Sclerites and Gula Controversy*

(a) *Terminology in the Literature*

Early workers did not always strictly define their terms and were at times uncertain and contradictory, so confusions developed.

Silfvenius (1905), in a general description of hydropsychid larvae, states that the hypostome is missing, yet later in the same paper (pp. 111–2), he maintains that in an undetermined species of *Hydropsyche* the narrow hypostome extends to the occipital foramen. Subsequently (Siltala, 1907)[5] he decides that the so-called hypostome in trichopterous larvae is not homologous throughout the series and that in the Hydropsychidae (he uses this term in the old, wide sense which included the philopotamids, polycentropids and psychomyids as well as the present hydropsychids *s.s.*) the sclerite which had been described as the hypostome by Klapalek (1888) and by himself, is not equivalent to the hypostome of case-bearing larvae. He considers that in the Hydropsychidae (*s.l.*) the so-called hypostome is really a more anterior sclerite which he homologises with the labial cardo and which Orcutt (1934) has designated as submentum, although later work indicates that a submentum is derived at least in part from a labial sternite rather than from the cardines (a matter critically discussed by Das (1937 : 66–68)). Siltala maintains that within the Hydropsychidae (*s.l.*) the condition of the " labiocardine " sclerite may possibly indicate the way in which the hypostome was formed. In the Psychomyinae, the aboral border of the labial cardo is extended medianly so that it is somewhat differentiated from the larger part. In the Hydropsychinae also, the aboral part is extended but does not reach to the occipital foramen, except in the one undetermined species in which colour difference distinguishes the aboral from the oral part. In this one species of hydropsychid, Siltala maintains that one may speak of a hypostome, although he regards it as lacking in all the other hydropsychids (*s.l.*) and in the Hydroptilidae. In the Rhyacophilinae, he considers that, although the pleura border on one another for a long stretch posteriorly, a small triangular hypostome is present anteriorly and is differentiated from the labial cardo not only by colour but by a suture. The present writer, however, agrees with Orcutt (1934) in being unable to distinguish a suture, in the strictest usage of the term, but recognises a thickened ridge and distinction in colour. The significance of this will be discussed later. Siltala's line of

[5] Silfvenius changed his name to Siltala in 1906.

reasoning clearly shows that he regards the hypostome as derived from the labial cardo.

Krafka (1923) terms the sclerite in question the " gula " in all the Hydropsychidae, referring to an " open " or " closed " gula according to whether it does or does not reach to the occipital foramen. He maintains that, in some species of hydropsychids, the gula consists of two pieces formed by the ventral margins of the " vertex " coming together near the middle of the gula, cutting it into a cephalic and a caudal half.

Orcutt (1934) cites Siltala (1907) and writes of the " gula or hypostome ", obviously regarding the two terms as synonymous.

Now, according to Snodgrass (1935), the gula is " a median ventral plate of the head in some prognathous insects, formed by a sclerotization of the neck region *proximal to the posterior tentorial pits*, continuous with the postmentum or submentum " [the italics are mine]. In contradistinction he defines the hypostoma as " the part of the subgenal margin of the cranium posterior to the mandible, usually narrow, but sometimes extended mesially as a hypostomal plate, or as a hypostomal bridge in the ventral wall of the head ". In the Hydropsychidae there is no evidence of the controversial median sclerite having been derived as a hypostomal bridge from the hypostome of Snodgrass' definition, and if his definition is accepted, then it is probably best no longer to refer to this median sclerite as a hypostome.

Das (1937) maintains that the gula is totally absent in trichopterous larvae; his evidence is in agreement with the general statements of Snodgrass. He points out that Crampton's (1921 and 1928) attempt " to define the gula by drawing a line between the bases of the maxillary cardines is responsible for many of his misinterpretations of the sclerites of the labium ". Crampton (1928) himself admitted that in elucidating the homologies of these parts, he did not attempt to study musculature and that a study of muscle attachment was needed.

Nielsen (1942 and 1948) follows Crampton (1921) and Krafka (1923) in that he recognises a gula throughout his descriptions of caddis larvae. He also adopts the nomenclature which calls the eulabium or labial stipites the mentum instead of the prementum, a system little used now although, as Snodgrass points out, Kadic (1902) and Walker (1931) have shown it to be logical. It terms the entire basilabium the submentum, or, if it is subdivided, then its two sclerites become the primary and secondary submental plates. Evidently Nielsen does not recognise any subdivision of the basilabium in trichopterous larvae, for he never has more than a single submental plate and so finds it necessary to invoke a gula, albeit in an anterior position. The more usual terminology calls the eulabium the prementum and then when the basilabium (or postmentum) is subdivided, its two plates are known as the mentum and submentum. Nielsen's refutation of the terminology of Orcutt and of Siltala on the grounds that the submentum is a more distally situated sclerite is not necessarily valid.

Hickin (1946), while aware of Siltala's work, retains the term " gular sclerite " in all his papers and Philipson (1953) refers to the gular plate in his description of the larval *Hydropsyche instabilis*.

The identity of the prementum and postmentum (or its subdivision into mentum and submentum) can be worked out from the musculature. The application of this in the present investigation will be discussed later.

(b) *The Posterior Tentorial Pits*

The position of the posterior tentorial pits will be considered next, since according to Snodgrass (1935) these should determine the distal limit of any potential gula.

In the British species of *Hydropsyche*, *Cheumatopsyche* and *Diplectrona* larvae, the posterior tentorial pits are rather inconspicuous except in sections, but their position may readily be determined by dissection to find where the posterior arms of the tentorium join the head capsule, or seen in preparations of the head suitably treated

to show the tentorium. The general disposition of the incomplete tentorium of larval hydropsychids has been described in the section on the apotome, and is indicated in figures 3, 4 and 5. Each posterior arm arises from the posterior tentorial pit, situated on the posterior ventral surface of the head, in the inturned postoccipital shelf adjacent to the postoccipital suture, and slightly lateral to the mid-line (figs. 3, 4 and 10). Thus each posterior tentorial pit (*p.t.p.*) lies in the margin of the occipital foramen.

In larvae of *Rhyacophila dorsalis* the posterior tentorial pits (fig. 2, *p.t.p.*) have the same posterior position as in the hydropsychids, but they are more obviously in the postoccipital suture. This proximal position is true of all other caddis larvae which I have examined, the posterior tentorial pits being separated from the occipital foramen at most by the exceedingly narrow postocciput.

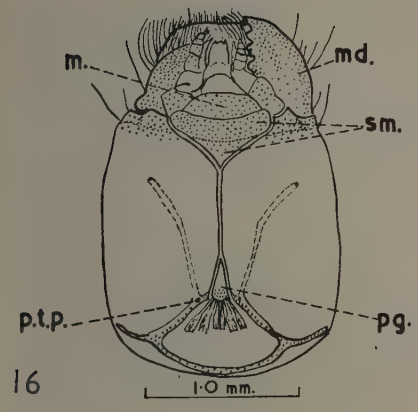
Since in all these forms the posterior tentorial pits are situated far posteriorly, frequently separated from the mouthparts by nearly the whole extent of the ventral surface of the cranium, the labium and any parts directly contiguous with it are well distal to the posterior tentorial pits. Hence none of these sclerites is strictly homologous with the gula as found in many Coleoptera and, on the basis of Snodgrass' definition, should not be termed a gula.

It seems probable that the ridge (fig. 2, *sm.r.*) which led Siltala to recognise a separate labial cardine sclerite and derived hypostome in forms like *Rhyacophila* larvae, is a secondary ridge across the submentum, a ridge serving to strengthen the head capsule ventrally between the mandibular articulations, *i.e.* comparable to the submarginal clypeal ridge on the dorsal aspect of the cranium. The submental ridge does not appear to serve for muscle attachment. I do not consider that the special development of a ridge necessarily justifies the recognition of separate sclerites and I regard the whole area as submentum. A similar ridge, although much less strongly developed, occurs across the submentum of the larval *Diplectrona felix* (fig. 16.)

(c) *The "Protogula", Ventral Margin of the Occipital Foramen, Postgenae and Phylogenetic Considerations*

In larvae of *Rhyacophila dorsalis* and in the known British larval species of *Hydropsyche*, also in *Cheumatopsyche lepida* larvae and the Japanese *Macronema radiatum*, there is a very minute sclerite (figs. 2 and 3, *pg.*) situated midventrally on the posterior margin of the head, separating the right and left postoccipital areas. As these postoccipital areas curve back from the ventral mid-line, this tiny midventral sclerite has its posterior margin at about the level of the posterior tentorial pits. It has often been overlooked, but corresponds to the anal gular sclerite depicted by Nielsen (1948 : 79, fig. 26) in *Oxyethira costalis* (Curt.) (in my opinion Nielsen's "gula" in *Oxyethira*, as in the other trichopterous larvae, should not be so termed). It is possible that this minute sclerite might represent a very rudimentary gula, yet it does not extend posteriorly (proximally) to the posterior tentorial pits as a definitive gula should ; even in fully grown larvae of the British hydropsychid *Diplectrona felix*, where it is larger (fig. 16, *pg.*), the extension is entirely distal to the posterior tentorial pits. For reasons which will become apparent later, I provisionally propose to refer to this sclerite as the protogula.

According to Krafka's (1923) view, this tiny protogula would be regarded as a now isolated part of what was once a continuous "open gula", extending to the occipital foramen, as described in Siltala's undetermined hydropsychid and by Krafka in an unidentified N. American species. Krafka considers the continuous "open gula" to be primitive and the condition where a proximal and a distal sclerite are present, separated from each other by the proximation of the two halves of the "vertex" at a midventral suture, to be a secondary, derived condition. In his opinion, the reduction of the proximal sclerite, with the result that no part of the gula borders the occipital foramen, *i.e.* his "closed gula" condition, is a further derivation.



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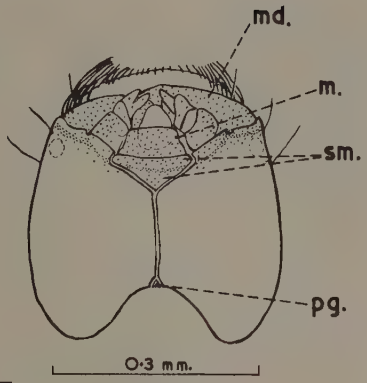

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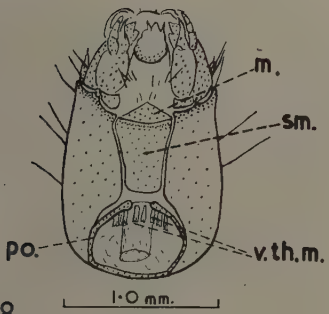

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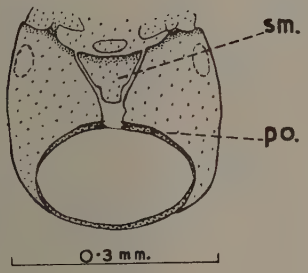

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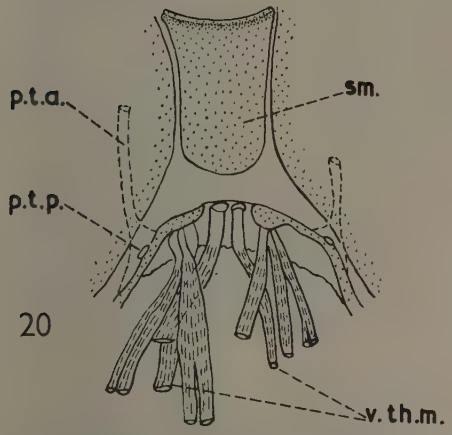

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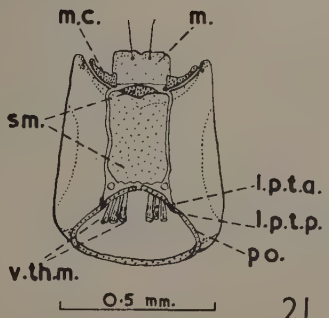

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FIGS. 16–21.—(16–17) *Diplectrona felix* McLach., ventral views of prognathous larval head: (16) last (fifth) larval instar, head treated to show tentorium; (17) second larval instar, external features of head. (18–20) *Molanna angustata* Curt., posterior views of hypognathous larval head: (18) fully grown larva, entire head; (19) first instar larva; (20) fully grown larva, preparation showing insertion of ventral thoracic muscles. (21) *Mystacides azurea* L., posterior view of head of fully grown larva.

Krafka regards the Leptoceridae as having an open gula and accordingly considers them to be the most primitive family of the Trichoptera (a view not generally held), while varying conditions are found within the Hydropsychidae.

If Krafka's " open gula " condition were primitive for Trichoptera, then one might possibly find it occurring in the earlier instars of those forms which have a " closed gula " in the fully-grown larva. At least one would not expect to find the parts of the " gula " relatively much smaller and more widely separated in the early instars than in the grown larva. Yet this is precisely what happens in the larva of *Diplectrona felix* (*cf.* fig. 17, second instar larva with fig. 16, fifth instar larva). In the second instar, the protogula is a minute sclerite, comparable with its condition in the fully-grown larvae of British species of *Hydropsyche*, yet in the fully-grown larva (fifth instar) of *Diplectrona felix*, the protogula is much larger, both relatively and absolutely, further incorporated into the head capsule and extending distally towards the submentum (the other part of Krafka's gula). Moreover, in the development of larvae of the British species of *Hydropsyche*, there is nothing to show that the submentum and protogula are the remains of one originally large, continuous sclerite, for in the first instar neither the submentum nor protogula are relatively more extensive than in the fifth instar; the disposition of labial and other sclerites on the ventral surface of the head is just the same in all larval instars. All this is in agreement with the statement of Nielsen (1942 : 269) that Krafka's theory is untenable, since, even in forms in which the well-developed larva has an extensive trapezoidal " gula " bordering the occipital foramen, it is triangular in the first larval instar, with only the point directed posteriorly. Nielsen (1936) has found this in *Oligoplectrum* and Siltala (1907) has demonstrated it in *Molanna*, where I have confirmed it. Thus, I am not aware of any developmental evidence within the Trichoptera to indicate that a condition in which the submentum (gula of other writers) extensively borders the occipital foramen is primitive for the group and that it subsequently became divided and reduced.

General evidence regarding the origin of the true gula in insects seems controversial. Snodgrass in his earlier work (1928), clearly considered it to be a derivative of the proximal part of the submentum, but according to his later (1935) definition, it is " formed by a sclerotization of the neck region . . . ".

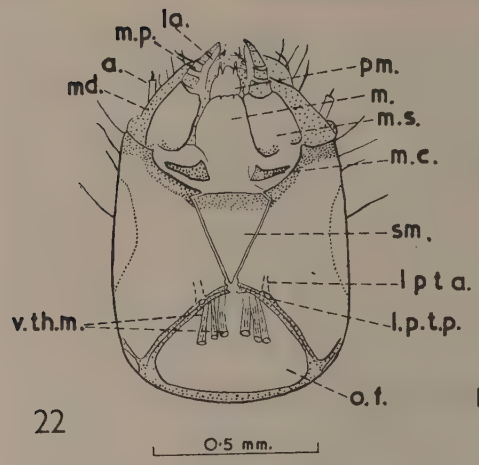
In my opinion, evidence from comparative anatomy, as well as from the study of developmental stages, indicates that the protogula in hydropsychid larvae is not derived from a once continuous submentum (or " gula ") which originally extended to the occipital foramen. During these investigations there has been no chance of examining either the undetermined species of larval *Hydropsyche* which Siltala regarded as having a hypostome, or the American hydropsychids with an " open gula " depicted by Krafka (1923) and by Ross (1944). However, similar conditions in other families have been studied. Krafka maintained that larvae of the Leptoceridae show the greatest development of the " open type of gula " and that the " gula " of larvae of the Molannidae is " very much like that of *Mystacides* " (Leptoceridae). " They are roughly quadrilateral and distinctly of the open type " (Krafka, 1923).

Now the larva of *Molanna angustata* Curt. dwells in a portable, tubular type of case (with lateral flanges) and has a hypognathous head (in contrast to the prognathous head which is characteristic of campodeiform larvae of the Hydropsychidae, Rhyacophilidae, Philopotamidae, Polycentropidae, Psychomyidae and Hydroptilidae). It is in the hypognathous head that one would most expect to find a submentum constituting the ventral border of the occipital foramen as it does in Apterygota such as *Petrobius maritimus* (Leach) and in Orthoptera such as *Gryllulus domesticus* (L.). Yet this investigation has shown that, contrary to Krafka's results, the submentum does not do so in *Molanna* larvae, even in fully grown individuals where it is admittedly well developed and " roughly quadrilateral " (fig. 18). Even in these

larvae it does not reach the occipital foramen but is separated from it by what is apparently a ventral extension of the postocciput, constituting a sclerotised rim to the occipital foramen ventrally as well as dorsally. This applies to the first instar (fig. 19) as well as to the older larvae (fig. 18), the main difference being that in the first instar the submentum is triangular, with only the apex extending proximally, instead of quadrilateral. The tentorium consists of anterior and posterior arms on each side, connected by a slender tentorial bridge ; the posterior tentorial pits are situated in the postoccipital suture, proximally to the submentum (gula of Krafka). *Occipital* sclerotisation does not appear to extend round to the mid-line ventrally (posteriorly), *i.e.* the *postgenae* do not meet behind the submentum. Ventral thoracic muscles are inserted on the ventral rim of the postocciput ; they are even inserted in the mid-line where the sclerotisation is weaker (fig. 20, *v.th.m.*).

In well-grown larvae of *Mystacides azurea* (L.), as in *Molanna*, it seems that the quadrilateral submentum is separated from the occipital foramen by the postocciput to which ventral thoracic muscles are attached (fig. 21). Macdonald (1950) describes a narrow, transverse, bow-shaped sclerite proximally to his rectangular gular sclerite in this species but does not comment further upon it. Similarly Hickin (1946, 1953) depicts transverse sclerotisations proximally to the rectangular " gula " in *Mystacides nigra* (L.) and *M. longicornis* (L.). The postocciput apparently extends mid-ventrally in well-developed larvae of *Leptocerus aterrimus* Steph. (fig. 22), where the submentum is triangular, with the apex reaching to the postocciput. A post-occipital extension may also be recognised proximal to the rectangular submentum of larval *Triaenodes bicolor* (Curt.) (fig. 23). In the *Triaenodes* larvae particularly, a high degree of fusion has occurred between the proximal sclerotised rim (which in my opinion may represent postoccipital extension) and the submentum ; however, careful examination with adequate magnification reveals a fine suture between the two. In all these leptocerid larvae, ventral thoracic muscles (*v.th.m.*) are inserted on the postocciput or its apparent extension, not on the submentum. (A pair of muscle impressions, which are especially obvious medianly near the proximal base of the submentum in *Triaenodes* larvae, represent the origins of mouthpart muscles (*see below*, section on prementum) and do not relate to ventral thoracic muscles). Likewise in larvae of *Limnophilus rhombicus* (L.) (Limnophilidae) and in the sub-eruciform British phryganeid larvae (the condition in *Phryganea obsoleta* McLach. is depicted in fig. 24), no ventral thoracic muscles are inserted on the submentum, although its proximal point reaches well towards the occipital foramen, but these muscles go to the postocciput. An additional feature of interest in larval *Phryganea* is the longitudinal ridge on each postgena, lateral to the submentum. These ridges do not serve for muscle attachment but may strengthen a head which is not very heavily sclerotised on its posterior surface and which has a large occipital foramen. I wondered if the ridges might be regarded as hypostomal sulci but they are really situated more medianly than would be expected of a typical hypostomal sulcus ; also, among known British caddis larvae, their occurrence in precisely this manner is restricted to phryganeids, so they are probably best considered as special strengthening ridges.

In some hypognathous, tube-dwelling trichopterous larvae the submentum does not extend as far proximally as the postocciput. For instance, in the larval sericostomatids *Notidobia ciliaris* (L.) and *Goera pilosa* (Fab.), the postgenae meet proximally to the submentum as in many prognathous larvae. So, in these hypognathous heads, the submentum may extend towards the occipital foramen in varying degree but is always separated from that foramen at least by what appears to be the ventral extension of the postocciput, an extension which provides a sclerotised rim to which the ventral thoracic muscles are attached. This is in marked contrast to the Thysanura and orthopteroids, in which the submentum constitutes part of the occipital foramen. However, neither in these insects, which are generally considered



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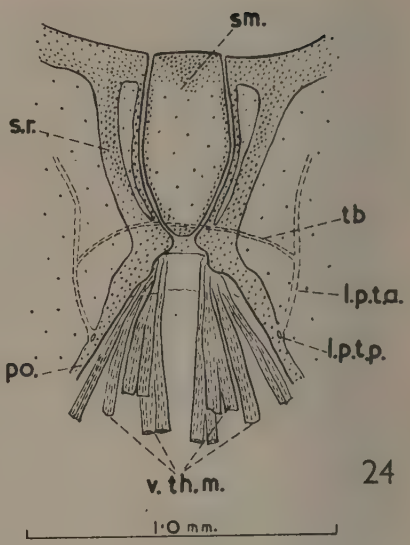

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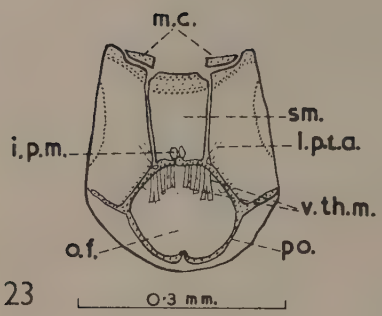

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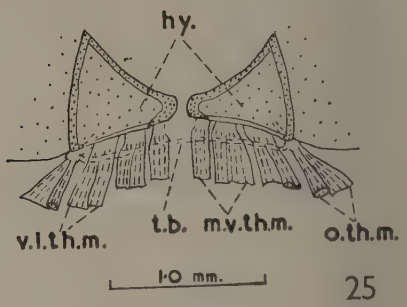

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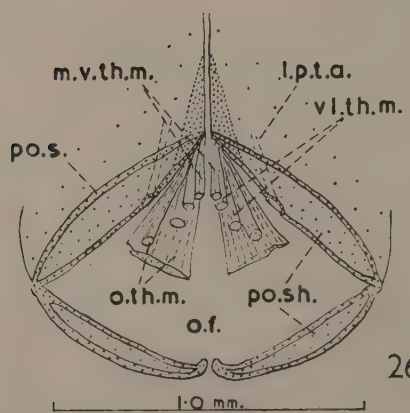

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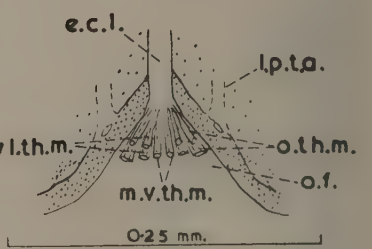

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FIGS. 22–27.—(22–25) Posterior views of heads of fully grown larvae showing insertions of ventral thoracic muscles: (22) *Leptocerus aterrimus* Steph.; (23) *Triaenodes bicolor* Curt.; (24) *Phryganea obsoleta* McLach.; (25) *Pieris brassicae* (L.). (26–27) Margin of occipital foramen and insertion of ventral thoracic muscles in fully grown larvae of: (26) *Philopotamus montanus* Don., and (27) *Agapetus fuscipes* Curt.

to represent the primitive condition in this respect, nor in the trichopterous larvae, do ventral thoracic muscles attach to the submentum. This feature is in agreement with the general statement of Snodgrass (1935 : 189) that ventral longitudinal or oblique horizontal muscles of the prothorax usually have their anterior attachment on the tentorial bridge, or some of them on cervical sclerites. The dorsal muscles from the thorax to the head are inserted on the postocciput. Concerning the Thysanura, Denis (1949, in Grassé) supports Chaudonneret's affirmation of the absence of muscles from the thorax to the submentum in *Thermobia* and in *Machilis*, saying that the longitudinal ventral muscles go to the metatentoria.

In trichopterous larvae, the tentorium is reduced to fibre-like anterior and posterior arms, with either a slender, fibrous tentorial bridge or none at all. The development of another attachment for the ventral thoracic muscles may perhaps be correlated with the reduction of the tentorium. Instead of going to the tentorium, these muscles are attached to the ventral margin of the occipital foramen. One can but speculate on which way round the correlation occurred : whether the reduction of the tentorium or the extension of the postocciput (and/or incorporation of cervical sclerites?) began to occur first, or whether they were both simultaneous ; the probability is that the exclusion of the submentum from the occipital foramen is a fairly primitive feature in larval Trichoptera, otherwise reduction of the tentorium might have resulted in the proximal border of the submentum taking over the insertion of ventral thoracic muscles. Also, the submentum is excluded from the occipital foramen even in first instar larvae (fig. 19, *Molanna*) and in the first instar of *Molanna* the proximal base of the submentum is less extensive, both relatively and absolutely, than in older larvae.

Reduction of the tentorium has occurred in many lepidopterous caterpillars. Short (1951) points out that " In caterpillars the tentorium is absent or weakly developed . . . The origin of the hypostomal bridge of caterpillars is perhaps connected with the poorly developed tentorial bar ". The head of caterpillars of *Pieris brassicae* has been studied in my investigation as a type for comparison with trichopterous larvae. In this example the head is typically hypognathous but hypostomal lobes are well developed and constitute the ventral margin of the occipital foramen, from which they separate all parts of the postmentum. Ventral thoracic muscles are attached to the hypostomal lobes (fig. 25). It seems that in lepidopterous caterpillars a need similar to that in trichopterous larvae has been met in a slightly different way. A hypostomal lobe is essentially a subgenal (or postgenal) area posterior to the mandible, usually offset by the so-called hypostomal suture (a ridge) which is that part of the subgenal sulcus behind the mandible. Typical hypostomal lobes are present in lepidopterous caterpillars ; however, in trichopterous larvae the head sclerotisations to which the ventral thoracic muscles may be attached arise behind the postoccipital suture and have no relation to any possible subgenal sulcus. One might regard them as arising *de novo* or as cervical sclerotisations which have become incorporated into the head—although from their general nature and relationship to the posterior tentorial pits, they have every appearance of being postoccipital extensions—but hardly as hypostomal lobes. The only regions of the ventral (or posterior) part of the larval caddis head which might, by analogy, be regarded as hypostomal areas, even in the absence of hypostomal sulci, are the more median parts of the postgenae ; and even where they extend fully medianly, meeting proximally to the submentum, apparently it is not to these that the ventral thoracic muscles attach in caddis larvae.

In all caddis larvae there has to be an adequate, suitably placed, head surface for the insertion of the thoracic muscles, but requirements and standards of adequacy may vary according to larval habits. Perhaps in the eruciform, tube-dwelling, hypognathous larvae, once reasonably adequate attachment has developed, there is no need for (or selection pressure in favour of) further increase in the degree of sclero-

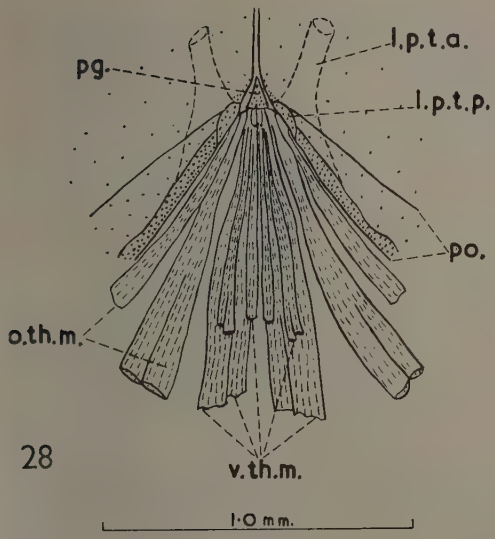
tisation ventrally around the occipital foramen. However, it is here suggested that this may be a matter of more importance in the prognathous head in which, consequent upon the well-known change of position and elongation of the ventral surface of the head, there is a change in the type of movement. Further, in some of the trichopterous larvae with prognathous heads, various features are found which can be interpreted as giving increased area or firmer attachment for muscles, and which may be correlated with habits.

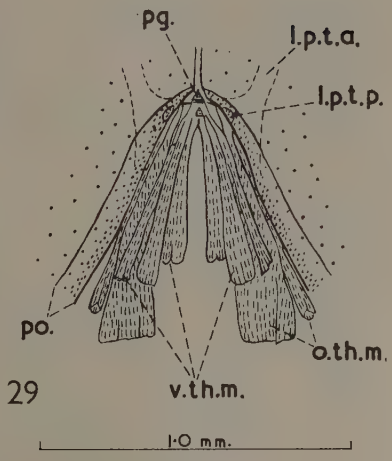
In philopotamid larvae such as *Philopotamus montanus* (Don.), there is a postoccipital ridge which is extended as a pronounced inturned shelf both dorsally and ventrally. This shelf tapers medianly but is still quite well developed in the midline and has powerful muscles inserted on its ridge mid-ventrally (fig. 26). There is a similar ventral postoccipital ridge in larval polycentropids,[6] psychomyids (e.g. *Lype* and *Tinodes*) and hydropsychids, but in these three families there is less development, *i.e.* more tapering away, of the shelf mid-ventrally. In larvae of *Rhyacophila dorsalis* there is no inturning of the postocciput as a ventral shelf and in Glossosomatinae (e.g. *Glossosoma boltoni* Curt. and *Agapetus fuscipes* Curt.) this shelf is but slightly developed. Now *Rhyacophila* larvae are caseless, predaceous forms which roam freely in swiftly flowing water ; the larvae of Glossosomatinae, although campodeiform, do build saddle-shaped, portable cases of sand grains and minute stones, scrape up diatoms and have a tendency to hold their prognathous heads in a hypognathous position. Neither the Rhyacophilinae nor the Glossosomatinae are net-spinners. It would seem, then, that the strong development of an inturned, ventral postoccipital shelf is associated with larvae of the four families that spin nets, webs, or galleries, and it may perhaps be correlated with movements of the head involved in performing this activity.

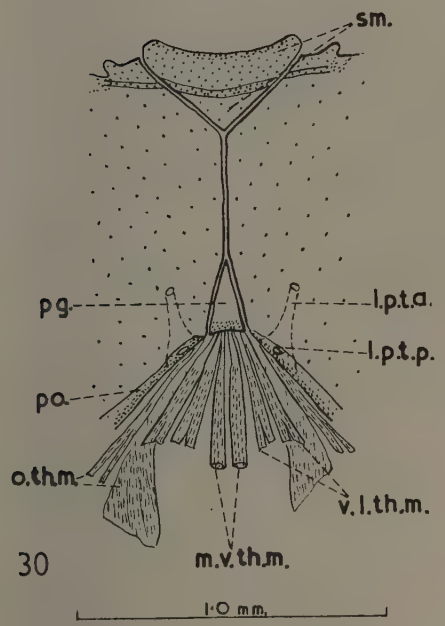
In the larvae of Glossosomatinae the postgenae meet at a mid-ventral suture (the ventral ecdysial cleavage line), the length of which separates the submentum from the occipital foramen, as in larval philopotamids, polycentropids, etc. Thoracic muscles are inserted on the postocciput, except in the mid-line, where (in *Agapetus*) some are attached to the cervical membrane at the proximal end of the median suture (fig. 27). This may represent a point of weakness under certain conditions and it is at this point that the protogula (Nielsen's anal gular sclerite) is developed in larvae of *Rhyacophila*, the Hydropsychidae and Hydroptilidae, and where even in *Glossosoma* there is a very minute pinpoint of sclerotisation. In *Rhyacophila*, *Hydropsyche* and *Cheumatopsyche* larvae, while some thoracic muscles are inserted on the ventrolateral margin of the postocciput, ventral ones (median and ventro-lateral) are attached at the mid-ventral point, *i.e.* to the minute protogula (figs. 28 and 29). In well-grown larvae of the hydropsychid *Diplectrona felix*, where the protogula is larger and further incorporated into the head capsule, its broader posterior border clearly serves for the attachment of muscles (fig. 30).

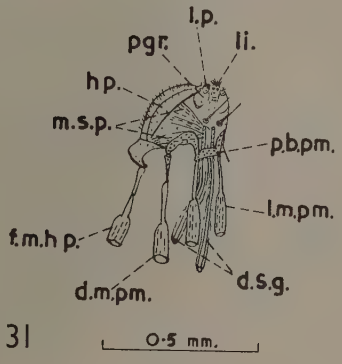
It is not intended to discuss in great detail the possible morphological origin of the protogula but rather to indicate a function for it and to show that it does not seem to be derived from a once continuous submentum. It may have arisen *de novo*, as the result of the pull of muscle attachment medianly, in the unsclerotised membrane between the two halves of the postocciput (for it is well known that sclerotisations tend to occur in the region of muscle attachments and their pull) or perhaps one could regard it as a small isolated piece of postoccipital sclerotisation, isolated because the ecdysial cleavage line has come to pass on either side of it. Alternatively, attempts might be made to homologise it with cervical sclerotisation, and this might bring it further into line with a definitive gula. Das (1937 : 70) maintains " that the gula is developed from the cervical membrane is shown by the fact that a pair of muscles arising upon the posterior border of the prothoracic segment is inserted

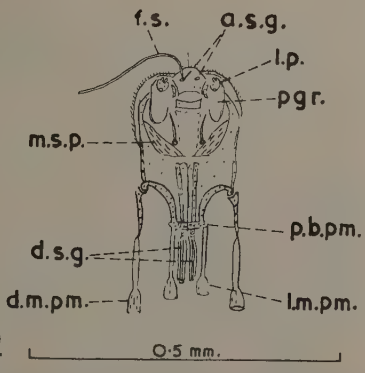
[6] Larvae of *Polycentropus flavomaculatus* (Pict.), *Plectrocnemia conspersa* (Curt.), *Neuriclipsis bimaculata* (L.), *Cyrnus flavidus* McLach. and *Holocentropus dubius* (Ramb.) were examined.











FIGS. 28–32.—(28–30) Ventral margin of occipital foramen and insertion of ventral thoracic muscles in heads of last larval instars of: (28) *Rhyacophila dorsalis* (Curt.); (29) *Hydropsyche instabilis* (Curt.); (30) *Diplectrona felix* McLach. (31) Ventrolateral view of prementum and ligula of fifth instar larva of *Hydropsyche instabilis*. (32) Ventral view of prementum and ligula of fifth instar larva of *Hydropsyche* sp

on a crescent-shaped groove in the anterior margin of the gula, just behind the pregula suture, in larval *Tenebrio*. These muscles are homologous with muscles having the same origin but inserted on the proximal border of the membrane just behind the submentum in certain larval insects where the gular area is not sclerotized ".

The possibility that the trichopterous protogula is derived from one member of a pair of cervical sclerites might be indicated by the presence of a very minute sclerotised patch which is to be seen just proximal to the protogula, but distinct from it, in larvae of *Hydropsyche*. However, this sclerotised patch might have no such significance.

Whether or not the protogula is to be regarded as a cervical sclerotisation, it is hardly a definitive gula, since it does not extend proximally to the posterior tentorial pits. However, it lies between them and has certain resemblances to a gula. It is arguable that the protogula is comparable to an early stage in the formation of a gula, a stage not carried any further in larval Trichoptera ; for in these larvae, if elongation of the ventral surface of the cranium occurs, it involves the postgenae, not the post-occipital region. If the postocciput were to become elongated (a purely hypothetical condition in trichopterous larvae), with the result that the posterior tentorial pits came to be situated in a relatively more distal position, away from the occipital foramen, and if the protogula retained its relation with the occipital foramen, it might then become elongated into a definitive gula, lying proximal to the posterior tentorial pits. It is with all these considerations in mind that I have provisionally called the sclerite a protogula.

The origin of the Trichoptera, affinities and evolution within the panorpoid complex are still controversial matters. It is generally agreed that the Trichoptera are related in some way to the other panorpoid orders and of recent years it has been customary to follow Handlirsch (1908) in deriving the Trichoptera (as also the Lepidoptera and Diptera) from the Mecoptera, a theory particularly strengthened by the extensive palaeontological work of Tillyard (1917–37, *see* bibliography in Grassé, 1951 ; Tillyard, 1933, is a useful summary) and supported by Grassé (1951), Imms (1944, 1957) and Ross (1956). However, Hinton (1958), on the basis of the anatomy of modern larvae, maintains that the Mecoptera are more specialised, possessing many characters which could not be ancestral to either Trichoptera or Lepidoptera, and he criticises Tillyard, Martynov and Carpenter for placing Permian and later ancestors of recent panorpoid orders together with the recent Mecoptera in one order.

While agreeing with Hinton about the principle of unequal development and recognising certain specialised features in modern mecopterous larvae which would preclude their being ancestral to Trichoptera, nevertheless I would re-emphasise the fact that there are certain similarities between Trichoptera and Mecoptera which probably indicate some measure of relationship, and that in some features both the developmental stages and the imagines of Trichoptera are more specialised than the Mecoptera. No ancestral larvae are actually known and it is not impossible that the Trichoptera might have stemmed from some ancestral mecopteran before the development of modern mecopterous specialisations. However in considering such matters, all types of evidence should be taken into account, and it is not proposed to embark on that here, but merely to discuss some aspects of the published descriptions of the larval Mecoptera, *Panorpa communis* L. and *Apterobittacus apterus*, which are relevant to the present study of the larval trichopterous head, and to indicate certain fundamental similarities.

In larvae of *Panorpa communis* and *Apterobittacus apterus*, although the head is hypognathous, the right and left genae and postgenae meet in a median suture posteriorly. Bierbrodt (1942) describes an incomplete occipital suture in larvae of *Panorpa communis*, pointing out that it is completely reduced orally, where a sutureless fusion between genae and postgenae results. The presence of any occipital

suture might be regarded as a primitive feature ; it is apparently lacking in larval Trichoptera. Bierbrodt, in his description of larval *Panorpa*, also mentions the occurrence of two further short sutures extending within the occiput from " the dorsal angles of the occipital foramen ". He points out that these sutures persist in the imago, although the occipital suture disappears and that Issiki (1933) has described similar sutures in *Micropteryx* and *Rhyacophila* (imagines). Bierbrodt maintains that the homologies of these sutures can be confirmed through the examination of the larva. However, in this respect the condition in larval *Panorpa*, which he studied, is probably more illuminating than that in larval *Rhyacophila*.

In larvae of *Rhyacophila dorsalis* there is a small heavily sclerotised ridge, or patch, extending from the " dorsal angle " of the occipital foramen, but it does not have the form of two distinct sutures or even sulci ; rather might it be the reduced basal stem from which sulci, such as those depicted by Bierbrodt in larval *Panorpa communis*, might arise or have arisen. (Following Snodgrass (1947), the term " sulcus " is preferred for those grooves and ridges which are not known to be genuine " sutures " in the strict usage of the word.) In all the known larvae of British hydropsychids there is a tiny ridge extending on to the occiput for a very short distance in this latero-dorsal position and ending in a nodule. Muscles (mandibular and thoracic) are attached to ridge and nodule. A very tiny ridge or nodule is likewise present at this point in some other larval Trichoptera such as *Agapetus fuscipes*, *Philopotamus montanus*, *Polycentropus flavomaculatus*, *Plectrocnemia conspersa*, *Odontocerum albicorne*, *Halesus* sp., *Phryganea varia* and *P. striata*. However in some other forms (e.g. *Molanna angustata* and *Anabolia nervosa*) there was not even a minute ridge or nodule to mark the position. Among the caddis larvae studied in this respect, only in leptocerids (*Leptocerus aterrimus*, *Triaenodes bicolor* and *Mystacides azurea* were examined) was there a well-developed sulcus, in the form of a groove or line of weakness, rather than a ridge, extending from the laterodorsal angle of the occipital foramen. This sulcus traversed the length of the head laterally until, in the oral region (in front of the eye), it curves anteriorly to reach the epistomal sulcus in the ecdysial cleavage line bounding the apotome. I am uncertain of the significance of this sulcus but probably, at least in its posterior part, it should be regarded as a sulcus separating occiput and postgenae.

Bierbrodt designates the ventral part of the occiput, *i.e.* the areas of the posterior surface of the head on either side of the median suture, as " gular regions " in larval *Panorpa* in preference to using the term " gula ". I would disagree with the use of either, for he depicts the posterior tentorial pits proximally to this region, close to the occipital foramen, just as in larval Trichoptera. Applegarth (1939), in his description of larval *Apterobittacus apterus*, refers to the postgenal regions on either side of the median suture as " hypostomal areas ", saying that they " form a hypostomal bridge through which extends a median suture that marks the line of closure ". Neither Bierbrodt nor Applegarth portray any hypostomal sulcus in the mecopterous larvae which they describe, but nevertheless these median posterior areas of the cranium might reasonably be called hypostomal areas by analogy, as discussed above in connection with trichopterous larvae, with which they are exactly comparable in this respect. One might even recognise a hypostomal bridge in the larval Sericostomatinae, where the postgenae fuse together behind the submentum, a median cleavage line being absent. However, in the absence of a hypostomal sulcus, I have some personal preference for the terms genae or postgenae.

Whatever the terminology one employs, there is a marked similarity between the posterior surface of the larval head of a eumecopteran and that of a trichopteran such as a glossosomatinid. Larvae of the Glossosomatinae have generally been regarded as belonging to the campodeiform group (Ulmer, 1909) and having prognathous heads, although they build cases. However Hickin (1943) says of *Agapetus fuscipes* : " Larvae eruciform. Head orthocentrous ", but in his drawing it appears

more procentrous. Certainly, even if one considers the larval glossosomatinid head to be really prognathous, one can say that it may often be held in an apparently hypognathous position and that in this group the condition is not entirely clear-cut but somewhat intermediate between the typical campodeiform and typical eruciform larvae. The relatively stout (for larval Trichoptera) tentorial bridge is probably a primitive feature. A tentorial bridge is also present in larval Mecoptera ; in *Apteropittacus*, Applegarth describes it as being formed by fusion of the tentorial arms close to the occipital foramen.

The Trichoptera are also considered to have affinities with the Lepidoptera, although the precise nature of the affinity is debatable. The relationship between the Trichoptera and the Lepidoptera is a large problem requiring discussion of a wide range of evidence with which it is not proposed to deal in this paper. However, some comparisons of parts of the larval heads have been made and a further point may here be indicated. The Micropterygidae have generally been regarded as the most primitive family of living Lepidoptera, although Hinton (1946, 1958) would reintroduce Chapman's (1917) proposal to raise the Micropterygidae to ordinal rank as Zeugloptera, and considers the group to be more closely related to the Trichoptera than to the Lepidoptera. Whether or not one separates the Micropterygidae from the Lepidoptera, the larva does seem to represent a primitive type of caterpillar and it is interesting to note that the head of *Micropteryx* is of prognathous shape, with the posterior surface ventral and elongated, the occipital foramen being situated far back ; the submentum, however, extends posteriorly.

One cannot say with certainty whether the primitive caddis larva had a hypognathous or prognathous head, but the evidence put forward in this paper suggests that a tendency to prognathism may have developed early on and rapidly become specialised in one line of caddis evolution. In another main line—that of larvae building portable, tubular cases and having hypognathous heads—the ontogenetical and morphological evidence suggests that a submentum with a broad proximal base is a secondary feature imposed on a head in which the postocciput had come to encircle the occipital foramen and the postgenae met posteriorly in a median suture.

However, so great is the diversity that can be found in the extent of the submentum (gula or gular sclerite of many previous writers) even within one family that, despite Krafka's attempts, its condition is probably not a character which can be used reliably for considering phylogenetic sequences, and affinities within the order. Certainly it should not be used on its own, but should be considered in relation to many other types of evidence. It is hoped that it may be possible to investigate some wider aspects of trichopteran evolution later.

(d) *The Prementum, Postmentum and Hypopharynx*

As regards the interpretation of the more anterior sclerites of the labium, the prementum can be recognised readily by the insertion of the premental muscles upon its proximal border, which is relatively heavily sclerotised in all the larvae of the British species of *Hydropsyche* (figs. 9, 31). Median muscles of the prementum appear to be absent in larval hydropsychids ; the muscles (*l.m.pm.*) inserted at each side of the ventral proximal border of the prementum must be the lateral muscles of the prementum. These lateral muscles of larval hydropsychids do not originate on either the submentum or tentorial bridge (the latter being absent in hydropsychid larvae), as described for some orders of insects, but are long muscles coming from the posterior ventral margin of the cranium, near to the occipital foramen (fig. 10, *l.m.pm.*). Each muscle is double, and Hinton (1958) maintains that " In Trichoptera the smaller of the two arises on the extreme base of the tentorium and the larger beside it on the postoccipital ridge ". I have confirmed this in hydropsychid larvae.

Dorsal muscles of the prementum arise nearby on the postocciput and are inserted upon the dorsal arms of the heavily sclerotised posterior border of the prementum (figs. 9 and 31, *d.m.pm.*).

The hypopharynx is fused with the dorsal aspect of the prementum and ligula, forming a composite structure on which open the salivary (spinning) glands. The proximal part of the hypopharynx bears a pair of more heavily sclerotised rods, or suspensoria, upon which are inserted the frontal muscles of the hypopharynx (fig. 31).

In hydropsychid larvae, posterior (proximal) to the insertion of the premental muscles and distal to the midventral suture (or ecdysial cleavage line), the area is the basilabium (or postmentum). According to the present interpretation, it cannot contain a gula, since it is far distal to the posterior tentorial pits. Anteriorly there is a membranous region, behind which the postmentum is divided into two sclerotised plates, namely the mentum, which is deeply notched anteriorly in species of *Hydropsyche* (figs. 3 and 9, *m.*), and, proximally to it, the submentum (*sm.*). The membranous region may be hidden under the mentum as in figure 9, owing to retraction. Some caddis larvae have a mentum consisting of two separate sclerites (left and right) e.g. *Agapetus fuscipes*, *Glossosoma boltoni*, *Tinodes waeneri* (L.) and *Notidobia ciliaris*. Sometimes the basal sclerites of the prementum are paired, as in *Rhyacophila dorsalis*. In many insects where the postmentum is divided into distinct mental and submental sclerotisations, the mentum may be identified by the insertion of the submento-mental muscles on its proximal border and by its position proximal to the insertion of the premental muscles, whereas the submentum has upon it the origins of the submento-mental muscles and of some of the premental muscles. However, no muscles have been found arising from or inserted upon either of these plates in the hydropsychid larvae examined. Both the submento-mental muscles and the median muscles of the prementum are absent. Das (1937) did not find submento-mental muscles in larval Trichoptera but he does depict median muscles of the prementum in larvae of *Anabolia*. Since it is quite common for some of the premental muscles to be absent, or to originate on the tentorium instead of on the postmentum (Das), the absence of the median muscles of the prementum in *Hydropsyche* larvae need not cause any doubt about the identification of the postmental sclerites. Hinton (1958) states that postmental muscles are absent in all panorpoid larvae except a few Trichoptera (some Rhyacophilidae and Polycentropidae) in which he found that the insertions of the tentorial adductors of the stipes were secondarily displaced on to the mentum. As indicated earlier, there is, however, another instance of muscles being attached to the postmentum in larval Trichoptera for, at least in *Triaenodes bicolor* among the Leptoceridae, a pair of muscles which seem to go to the prementum originate medianly on the proximal base of the submentum; (the muscle impressions are shown on the submentum in fig. 23.) Unfortunately in my limited material I did not succeed in elucidating precisely which premental muscles these are. Other muscles of the maxillo-labium originated near by, but on the ridge constituting the margin of the occipital foramen—the ridge which is apparently postoccipital extension —and not on the submentum.

As discussed above in the section on the posterior tentorial pits, in my opinion the ridge crossing the submentum in forms such as *Rhyacophila dorsalis* and *Diplectrona felix* is a secondary strengthening feature within the submentum, acting as a brace between the bases of the mandibles, and is not delineating separate sclerites. It is not accompanied by any suture.

The present investigations have shown that the degree and pattern of pigmentation and sclerotisation of the mentum is not uniform throughout the genus *Hydropsyche* and is of use in determining larval species. Details of this will be given elsewhere. The terminology adopted for these labial and head sclerites will be as indicated above and in the figures.

(2) *The Labial Palps*

Silfvenius (1905) describes a labial palp of two segments in hydropsychid larvae, but both Das (1937) and Nielsen (1942) recognise in trichopterous larvae a region of the prementum (mentum of Nielsen) differentiated as a palpiger, and say that it bears a palp of one segment. Hickin (1946) considers that the labial palp generally consists of two segments, implying that the basal segment is not a palpiger.

The labial palp is very rudimentary in larval *Hydropsyche* and I hesitate to express a definite opinion in the controversy based on hydropsychid material. However, in *Hydropsyche* larvae the demarcation between potential palpiger and prementum is indefinite and not nearly as distinct as that between " palpiger " and palp (fig. 32). So on these grounds, although superficial, the recognition of a palpiger and a palp consisting of one segment may perhaps be justified. Distally, the palp bears the usual sensilla. Even in larvae of *Rhyacophila dorsalis* and *Notidobia ciliaris*, which have relatively larger labial palps, it is difficult to make out the exact condition with certainty and I have failed to detect any palpal muscles. Hinton (1958) maintains that muscles are absent in the labial palps of larvae of all recent panorpoid orders.

Hinton also says that labial palps are absent in larvae of some Polycentropidae. In this family I have found labial palps present in larvae of *Plectrocnemia conspersa*, *Polycentropus flavomaculatus*, *Cyrnus flavidus* and *Holocentropus dubius*. These palps are, however, closely compressed against the ligula and are rather difficult to see (especially in *Holocentropus dubius*) unless one removes the maxillolabium and has adequate magnification.

Although not entirely certain about the parts of the labial palp in caddis larvae, I propose to follow the terminology of Das and of Nielsen in this instance and refer to a palpiger and a palp of one segment in my larval descriptions.

VI. Acknowledgments

Dr. J. W. H. Lawson kindly criticised an early draft of this paper and I subsequently enjoyed profitable discussion with him and Mr. R. A. Crowson, both of whom read the final manuscript. Much of the discussion centred round an evolutionary theme and has been excluded from this paper but I hope that they will see the full benefit of it later. Dr. H. D. Slack supplied encouragement, larvae of *Mystacides azurea* and *Glossosoma boltoni* and also advice about drawings. Mr. A. R. Tindall kindly sent samples of his specially fine tungsten needles to me and these were used in some of my remaining microdissections. Mr. C. R. Towns took the photograph which appears as Plate I, and Mr. D. B. Williams assisted with stencilling lettering on to the figures. The University College of North Staffordshire provided equipment and facilities for the work.

It is a pleasure to express my grateful thanks to all these.

VII. Summary

Some controversial matters in the morphology of the head and mouthparts of larval Trichoptera have been discussed. The investigations were made with special reference to the Hydropsychidae but other larvae were also studied for comparison.

The main points arising from the investigations are as follows :

1. The form of the tentorium differs slightly within the various larval Trichoptera. In most larvae a tentorial bridge is present—relatively stout in a few (*e.g.* Glossosomatinae), very slender in the majority—but it is absent in some (as in British Hydropsychidae).

2. The location of the anterior tentorial pits and of the incomplete epistomal sulcus in hydropsychid larvae, also the disposition of muscle attachments relative to the position of the frontal ganglion, all indicate that the facial apotome is fronto-

clypeal in larval Trichoptera. An anterior (distal) ridge is interpreted as a submarginal clypeal ridge.

3. The disposition of sclerites and the relevant musculature in the maxilla of some larvae of Trichoptera and other panorpoid orders has been considered. It is thought preferable not to regard the stipes as divided into basi- and dististipes, and a palpifer is not recognised in these forms. The dististipes, or palpifer, of some writers is really the basal segment of the palp, which has fused with the lobe and partially embraces it, a view strengthened by the additional fusion of the next distal segment of the palp with the lobe in at least hydropsychids, polycentropids and *Rhyacophila*. In these larvae the maxillary palp is interpreted as consisting of five segments, not four, and as being subtended by an undivided stipes. The maxillary lobe of larval Trichoptera represents a lacinia.

4. The position of the posterior tentorial pits shows that a gula is absent in all the larval Trichoptera investigated. The sclerite often referred to as a gula is really the submentum. The submentum may have a secondary strengthening ridge which gives the appearance of subdividing it.

5. In the larval heads of the British Hydropsychidae, Hydroptilidae and *Rhyacophila*, there is a small, often minute, sclerite situated posteriorly in the midventral ecdysial cleavage line, with its proximal limit at about the level of the posterior tentorial pits. Owing to its position relative to the tentorial pits it is not a definitive gula, although evidence from the comparative morphology of muscle attachments suggests some affinity with a gula. Ontogenetic evidence does not support its derivation from a once extensive submentum, but it is an open question whether it is to be regarded as a cervical sclerotisation incorporated into the head capsule, a piece of postocciput or a new formation resulting from the pull of muscles in that region. It serves for the insertion of ventral thoracic muscles, for which it provides firmer attachment at the mid-ventral point of the margin of the occipital foramen, a point of weakness in these larvae. This sclerite is provisionally termed the protogula. Hypothetically it might develop into a definitive gula if the postoccipital region were to elongate.

6. The insertion of ventral thoracic muscles has been considered in the heads of some other caddis larvae. It is suggested that the slender nature of the tentorial bridge, or its loss, may be associated with other provision for these muscles. Firm attachment, often provided by an in-turned, ventral postoccipital shelf, seems to be of particular importance in net-spinning larvae. It is shown that even in those hypognathous, tube-dwelling forms in which the submentum was thought to border the occipital foramen (e.g. *Molanna* and *Mystacides*), ventral thoracic muscles are not inserted on the submentum, which is in fact separated from the foramen by other sclerotisations that may be postoccipital extensions. A submentum reaching extensively towards the occipital foramen is here regarded as a secondary condition in those caddis larvae in which it occurs.

7. The submentum is not a hypostome, and typical hypostomal sulci are lacking in larval Trichoptera. If hypostomal areas are to be recognised in these larvae, then by analogy it is the postgenal areas on either side of the submentum or of the midventral suture which might be so termed.

8. Some similarities with larval heads of other insect orders are indicated and the phylogenetic position is mentioned, but it is felt that full discussion of the phylogenetic implications should be postponed until other types of evidence than that from controversial points in larval heads can be incorporated.

9. The identity of prementum, mentum, submentum and hypopharynx is established in hydropsychid larvae from a study of their muscle attachments (or absence of them). Some comparisons with other larval Trichoptera are indicated.

10. The labial palps were studied in larval hydropsychids, *Rhyacophila* and poly-

centropids. Probably in these forms the palp consists of one segment only and a palpiger is present.

The object of this paper was to examine the confusions of morphological terminology and statement which occur in the literature describing larval Trichoptera when portions of the head or mouthparts are mentioned. An attempt has been made to provide clarification and morphological justification for the terms which this writer proposes to use in future descriptions of caddis larvae. Certain phylogenetic implications have emerged and it is hoped to discuss and test these in a later paper where they can be considered in a wider context.

VIII. Abbreviations Used in the Figures

a., antenna
acl., anteclypeus
acl.m., anteclypeal muscles
a.l.m., anterior labral muscle (dorsal labral retractor)
a.s.g., apertures of silk glands
a.t.p., anterior tentorial pit
cb.m., cibarial muscles
c.f.la., cranial flexor of lacinia
c.f.m.p., cranial flexor of maxillary palp
c.g., cerebral ganglia
d.m.p., depressor of maxillary palp
d.m.pm., dorsal muscle of prementum
d.s.g., ducts of silk glands
e.c.l., ecdysial cleavage line
e.s., epistomal sulcus
f.g., frontal ganglion
f.m.hp., frontal muscle of hypopharynx (mouth angle retractor)
f.s., filament of silk
g., galea
hp., hypopharynx
hy., hypostome
hy.s., hypostomal sulcus
i.p.m., impression of premental muscle
l., labrum
la., lacinia
l.a.t.a., left anterior tentorial arm
l.a.t.p., left anterior tentorial pit
li., ligula
l.l.m., lateral labral (tormal) muscle
l.m.p., levator of maxillary palp
l.m.pm., lateral muscle of prementum
l.p., labial palp
l.pc.p.m., lateral precerebral pharyngeal muscle
l.p.t.a., left posterior tentorial arm
l.p.t.p., left posterior tentorial pit
m., mentum
m.c., maxillary cardo
md., mandible
m.l., maxillary lobe
m.p., maxillary palp
m.s., maxillary stipes
m.s.p., muscles of silk press
m.v.th.m., median ventral thoracic muscles
o.f., occipital foramen
o.th.m., oblique thoracic muscles
p.b.pm., proximal border of prementum
pc.p.m., precerebral pharyngeal muscles
pg., protogula
pgr., palpiger
p.l.m., posterior labral muscle
pm., prementum
po., postocciput
po.s., postoccipital suture
po.sh., postoccipital shelf
p.t.p., posterior tentorial pit
s.c.r., submarginal clypeal ridge
s.f.la., stipital flexor of lacinia
sm., submentum
sm.r., submental ridge
s.r., strengthening ridge
t.ad.c., tentorial adductors of cardo
t.ad.s., tentorial adductors of stipes
t.b., tentorial bridge
v.th.m., ventral thoracic muscles
v.l.th.m., ventrolateral thoracic muscles

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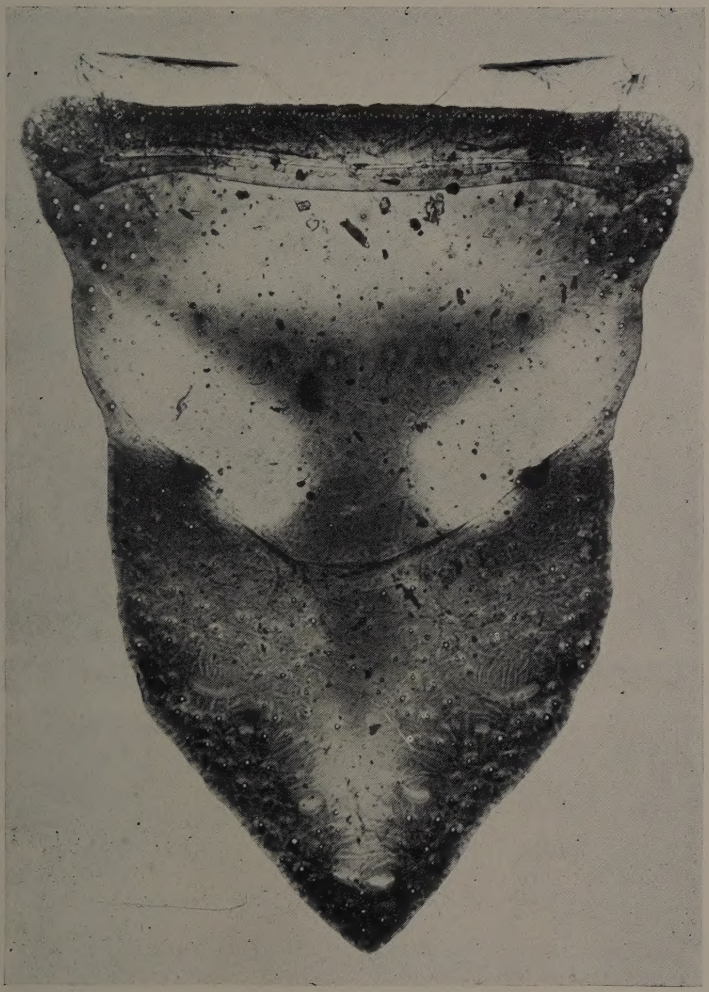
PLATE I

Apotome from the head of the last larval instar of *Hydropsyche pellucidula* (Curt.), showing muscle impressions. (*Photo:* C. R. Towns).



Apotome from the head of the last larval instar of *Hydropsyche pellucidula* (Curt.), showing muscle impressions. (*Photo:* C. R. Towns).